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CONTRIBUTIONS TO THE MORPHOLOGY AND TAXONOMY OF THE BRANCHIOPODA NOTOSTRACA, WITH SPECIAL REFERENCE TO THE NORTH AMERICAN SPECIES

By Folke Linder

INTRODUCTION

Since the days when Packard's "Monograph of the Phyllopod Crustacea of North America" was published (1883), the accessible material of notostracans has grown considerably, and the principles commonly used for the taxonomy have been discussed in several papers. Analyses of these characters, especially by Braem (1893), Gurney (1923, 1924), Sidorov (1927), Barnard (1929), and Gauthier (1934), have established a considerable variation in most of the characters of European, Asiatic, and African forms. This variation, of course, does not make a survey of the Notostraca of North America an easy task, and when I venture such a survey here, I wish to note that in some respects it is tentative only. It is based mainly upon a study of the collections of the U. S. National Museum, amounting to 109 lots and considerably more than 2,000 specimens. This study was performed during a 3 months' visit to the Museum in 1946, and was made possible by a grant from the Smithsonian Institution, to which my thanks are due for this generous support. I am also greatly indebted to Dr. Waldo L. Schmitt and other officials of the Museum for having most kindly facilitated my work. Also, Prof. J. E. Lynch, University of Washington, Seattle, kindly allowed me to examine some important material from the northwestern United States. For comparison I had specimens from other parts of the world, though this material, about 3,000 specimens from 71 localities, has not been as comprehensive as could be desired.

Gurney (1924, p. 559) says about the taxonomy of the Notostraca, "The separation of species within the genera *Apus* and *Lepidurus* is a matter of quite unusual difficulty, since there is much variation, and, as a rule, the only characters on which separation can be based are small and ill-defined." Barnard (1929, p. 230) agrees with him, and so do I.

As for other phyllopods, the females of the Anostraca present a similar difficulty, as, sometimes, if they occur without males, it is not even possible to say with certainty to what family they belong. But the males of this order give excellent specific characters in the genital organs and the second antennae—organs which display a striking uniformity in the Notostraca. In the Conchostraca, the structure of the head and the carapace provides rather good specific characters, but in these respects, too, the Notostraca are fairly consistent.

The characters actually employed—helpfully reviewed by Barnard (1929, pp. 230–234)—for the most part represent differences of degree only. A striking example of this is Packard's (1883, p. 319) key to the American species of *Apus;* a study of the type specimens of the species involved immediately reveals that the number of spines on the supra-anal plate, which seems to be the fixed point in this key, is not constant but overlaps the boundaries between his species. According to my experience, one seldom finds a specimen which is in complete accordance with the description of any of these species, and similar difficulties are met even when one goes to the type specimens. These are not numerous enough to cover the range of individual variation, nor are their descriptions extensive enough. Yet such variation is especially important when the characters involve differences of degree.

Of course, one can often compare material from neighboring localities in order to learn something of this variation, or, better still, one can try to get abundant material from the original locality. The first course is generally the only one practicable in museum work, and I have tried it here. It is not very satisfactory, though some results seem to be obtainable in this way.

Each sample of Notostraca ought to contain about 50 or more specimens in order to cover most of the variation. And, in my opinion, a new species should never be described from less than 100 specimens from the same district, preferably taken at varying times of the season. Paratypes are, in many respects, just as important as holotypes.

A special question arises when we try to interpret the variation. Ghighi (1924) suggests that the variation may sometimes be due to the presence of two species in the same pool. I think that this occurs only rarely, as in the Anostraca and in the Conchostraca, and if it should happen to occur in a particular sample, the fact would probably be readily revealed when all characters are considered. I have not found any indications of mixed populations in this sense in the samples I have examined, nor can I find any definite reference to it in the literature, with the exception that Lundblad (1920) noted that species of different genera sometimes have been found in the same pool. In these cases no intermediate forms are reported.

So far, I have considered only specific characters. Sidorov (1927) and Gauthier (1934) are convinced that there are geographical subspecies within *Apus cancriformis* of the Old World. I do not deny the possibility that there may be such taxonomic units in some North American species, most likely among the forms of *Apus*. Among the anostracans, which have similar habits, I have found some indications of geographical subspeciation in forms of the genera *Branchipus* and *Tanymastix* of the Old World. Smirnov (1931) seems to be of similar opinion with regard to some conchostracans.

However, I do not find it possible to separate geographical units out of the material to which I have had access. In my opinion the appropriate way of doing this would be to investigate thoroughly some limited areas, and to follow this with a comparison of samples from interspersed districts. The possible existence of clines (Huxley, 1942, and Margalef, 1948) might also be traced in this way.

During my work it appeared that a species from Asia and Europe, *Lepidurus macrurus*, is a synonym of the American species *L. couesii*. Further, I found that South American forms of *Apus* are the same species as the North American *Apus longicaudatus*. This may be significant. It is worth noting that no one since the days of Packard (1883) and Simon (1886) has tried to compare species from all over the world, and, with our present knowledge of the great latitude in variation of many characters, it does not seem at all improbable that additional species from different continents will be found synonymous.

The present tendency to reduce the number of species in the Notostraca (see Gurney, 1924, and Barnard, 1929) is, I think, sound, and is well supported by our present knowledge of variation. This paper follows the same line.

In the following pages I have tried to analyze, with the help of material from all continents, the commonly used taxonomic characters and, also, a character which has been very much neglected, the number of body-rings of different kinds. This character has proved quite useful. One of the results is a new grouping of the species of *Lepidurus* into what seems to be two natural groups; another, that lower taxonomic units begin to be revealed among parthenogenetic populations, although the real status of these cannot be determined from the accessible material. In connection with this analysis I have also considered polypody, and the peculiar phenomenon I have called spiral growth, both of which are problems of interest from a more strictly morphological point of view. Finally, I have applied to the North American material the results of this analysis of taxonomic characters.

TERMINOLOGY AND MEASUREMENTS

Instead of the term "segment," in referring to the postmaxillary part of the animal, I prefer the term "body-ring." The first 11 body-rings I call the thorax. This is followed by the abdomen, which is comprised of leg-bearing body-rings, legless body-rings, and the telson, which is not a true segment, and which should not be included in the number of body-rings. The series of legs does not always stop underneath a boundary between two body-rings; it may stop at any place quite independent of these boundaries (fig. 20). I have found it advisable to count half leg-bearing body-rings in those cases where the series stops approximately underneath the center of a ring, and a whole leg-bearing ring when the series covers almost the whole ring, disregarding those cases where the series only slightly surpasses a boundary. Incomplete rings (fig. 16) are often found at the anterior boundary of the telson, but very rarely within the series of rings.

It is useful to have a short formula when describing the numbers of the various kinds of body-rings in a specimen or in a species. In this paper, I have used such an arrangement. Thus, the formula 11+12+5=28 body-rings indicates that there are 11 thoracic, 12 abdominal leg-bearing, and 5 abdominal legless rings, forming a total number of 28 rings (telson not included). For a species the formula is more complicated because there is a considerable variation of these numbers within the limits of a species (Linder, 1947). If the abdominal leg-bearing rings number from 16 to 18.5, the legless rings from 5 to 10, and the total from 35 to 38 rings, the formula would be, 11+(16–18.5)+(5–10)=35–38 body-rings. If there is an incomplete ring, the abbreviation "i" is inserted, as in this example: 11+12+5+i=28+i body-rings. It is also possible to indicate the presence of the interesting abnormality, spiral growth, and its place within the series. If a spiral of 3 rounds appears after the 25th body-ring, immediately followed by the telson, in a specimen with 12 abdominal leg-bearing rings, the formula would run as follows: 11+12+2+sp.3r.=25+sp.3r.

The telson bears a rather neglected structure, viz, a pair of dorsal sensory setae (fig. 28), surrounded by short spines, and a pair of caudal filaments. Between the latter there is, in the genus *Lepidurus*, the supra-anal plate. I measure the length of this plate from the most anterior point of the basis of the caudal filaments to its apex.

As Barnard (1929) and Sømme (1934) have pointed out, the total length of an animal cannot be measured with proper accuracy in preserved material. The reason is simple enough. Anteriorly and posteriorly, the integument of a ring is much softer than in the central part. This soft integument may form a fold directed inward and forward, and in such cases the rings appear short and the total length of the animal is relatively short, too. But other specimens from the same lot, which have a carapace of similar length, may show no deep fold in these places, the soft integument being more or less stretched out between the more highly chitinized parts of the rings (fig. 1). In

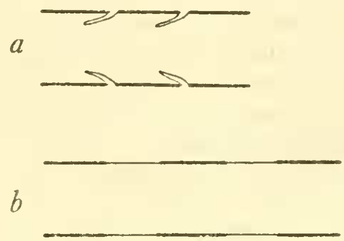

FIGURE 1.—Schematic diagram of the body-rings of a notostracan showing how the length is influenced by varying contraction. Highly chitinized parts of the integument indicated by heavy lines. *a*, Contracted; *b*, extended.

the latter case, of course, the rings appear longer and the total length of the animal may be considerably greater than in the former cases. It is quite usual to meet with both extremes and a more or less continuous series of intermediate cases in a lot containing a large number of specimens, as they may have been fixed in varying stages of contraction. Rosenberg (1947) noticed a considerable shrinking of the specimens when they were placed in preservation fluid. It is also obvious that preservation, after an indeterminable time, weakens the soft tissue in and between the body-rings and thus causes a lengthening of the body to a variable degree. In very old material maceration (and lengthening) may have gone rather far. It is, however, desirable to give an idea of the length even if it cannot be accurately stated. I measure the length on the midline from the apex of the head to the base of the caudal filaments. Thus, in *Lepidurus*, the length of the supra-anal plate is not included in the figure of the total length. This may seem a little odd, but in this way comparable figures for *Lepidurus* and *Apus* are obtained. The length of the supra-anal plate in the former genus may be up to 44 percent of the length of the carapace, and thus it would be quite misleading to include this plate, which has no counterpart within the genus *Apus*.

Barnard (1929) also points out that we cannot give an accurate count of the body-rings exposed behind the carapace. In order to give some, even if not an accurate, idea of this conspicuous feature I have mentioned the number in some specimens. But I give this number, as well as the figures of the total length, only with a stated reservation as to its accuracy.

As Sømme (1934) has shown for *Lepidurus arcticus*, the carapace is little affected by the preservation fluid and thus can give an idea of the size of the animal. This is only natural, because it is continuously and highly chitinized. Following the general custom, I measure its length along the mid-dorsal line. Of course, we cannot be sure that variations in this figure closely follow the variations of the real total length of the body; the relation may vary according to varying ages of the specimens, to say nothing of the varying contraction. To obtain the greatest width of the carapace, the usual method seems to have been to measure it in a straight line. This is not reasonably accurate, because the height of the carapace may vary, sometimes to a considerable degree. It is better to measure the greatest width from the carina to both sides (fig. 2). In cases of

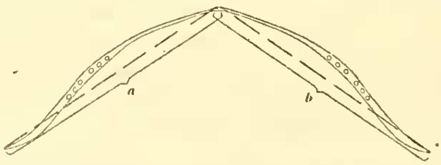

FIGURE 2.—Cross section of the carapace of a notostracan, showing how the width of the carapace is measured.

distortion, I have flattened the carapace to a shape similar to normal appearance before taking the measurement.

I count 5 endites on each leg (fig. 26). The coxal lobe is the first endite; it is essentially similar to the other endites in the arrangement of the setae and has on its margin similar small elevations covered with small needlelike structures. What Packard (1883) calls the sixth endite is quite dissimilar to the more basal, real endites; it has only a single row of setae and spines along its margin, and no trace of the small elevations mentioned above; I call it the endopodite, as many other authors do. Packard's "flabellum" is the exopodite, and his "gill" is called epipodite in this paper. Further, we sometimes find what may be the vestige of a preepipodite (fig. 22) in the form of a small elevation with a few setae (cf. Eriksson, 1934, p. 236).

Specimens from the following museums were examined:

Muséum National d'Histoire Naturelle, Paris (Paris Mus.).
Naturhistoriska Riksmuseet, Stockholm (Stockholm Mus.).
Zoologiska Museet, Kungl. Universitetet, Uppsala (Uppsala Mus.).
United States National Museum, Washington (U.S.N.M.).

BODY-RINGS AND POLYPODY

Following the usual custom, I consider the body proper to begin with the first postmaxillary ring, which is, however, strictly separated from the head only on the ventral side. Packard (1883) counts the first ten body-rings as the thorax, and the following ones as the abdomen. I include the eleventh body-ring in the thorax, as does Simon (1886) in his important revision of the phyllopods and as Sars does in his many descriptions of various notostracans. More than a hundred years ago Zaddach (1841) showed, in an admirable work now almost neglected, that the first 11 body-rings are essentially similar to each other in the equipment of muscles, while the following ones differ quite considerably from them. Further, the legs of this portion are different, though the boundary in this respect is usually not distinct. A boundary between different regions in this location is recognized in crustaceans of many orders—so many, in fact, that it is not likely to be a mere coincidence (Linder, 1941, p. 113).

I have abandoned the use of the term "segment," replacing it with the term "body-ring," when real rings or parts of rings are concerned. I do this for the reason that in the abdomen there are no complete, ordinary segments but two series of parts of segments, in some respects independent of each other—the series of rings and the series of legs. These are united to form a composite structure unique in appearance. This is the true meaning of the much discussed phenomenon, polypody. It is not an absolutely new view. Lankester (1904) expressed a similar view, but did not give evidence for his opinion. However, Zaddach (1841) had already supplied much evidence supporting that opinion, and the following facts, most of which have not been noticed by earlier authors, may give additional evidence:

1. The series of legs covers a varying number of body-rings in specimens from one locality. Zaddach (1841) has given an example of this. He also regards the number of pairs of legs as fixed; however, I have found that this number is subject to a considerable variation. The series of legs may stop at any place under a body-ring (fig. 20). If we choose a certain pair of legs in the caudal part of the series of legs, and determine its place under the series of body-rings, we shall find that it has varying positions in various specimens from the same locality (see table 2, p. 42). Thus, each body-ring in the abdomen does not have a fixed number of pairs of legs, and this means that there is no evident correlation, as is supposed by most authors, between the series of legs and the series of abdominal body-rings. Evidence for this fact from extra-American material is given in an earlier paper (Linder, 1947).

2. The boundaries between the body-rings in the leg-bearing part of the abdomen do not continue ventrally. They stop at a longitudi-

nal boundary, always well marked and often formed as a ridge in the integument (fig. 20), which delimits the leg-bearing area. This area may be divided into "segments" coinciding with the legs but totally independent of the boundaries between the body-rings. Zaddach (1841) has already described the ventral "segmentation" and the corresponding division of the longitudinal muscles in this area in *Apus cancriformis*.

3. In two cases of abnormal growth of the body-rings that I have found, the series of legs is not affected by the abnormal turns, or spiral growth, of the related body-rings (fig. 17).

The first two points hold good for each of the species of Notostraca that I have examined, though some of the details may be difficult to observe in specimens which have just molted or are badly preserved.

It is a well-known fact that the rate of production of new body-rings (in early postembryonic stages) is quite different from that of the legs, with their muscles and nerve-cord ganglions. From the caudal end of the series of legs there are produced, at an almost frantic rate and in considerable number, the elements of the leg-bearing area, but the body-rings, budding from the anterior margin of the telson, increase in number relatively slowly. The body-rings do not vary much in size, but the elements of the leg-bearing area grow smaller and smaller caudally, as if the animal meets the frantic activity of this part with something like starvation of its individual elements. We might assume a kind of organizer at the end of the series of legs (for what else could we assume?) that is, in some way or other, less favored than the ordinary organizers at the anterior boundary of the telson.

I have noticed in many specimens that this disproportionate development has continued during the further growth of the animal. Thus, we often notice that in a larger animal the series of legs covers a smaller number of body-rings than is the case in a smaller animal in the same lot (see table 2), indicating that the size of the body-rings, but not necessarily their number, increases faster than does the series of legs. Other facts also point to this conclusion: an oblique striation occurring at the area where the body-rings and the series of legs meet, explained as the mark of a tension between the two parts as they grow at dissimilar rates; and the moving forward of the fiftieth pair of legs, as observed in table 2 (we note that this moving forward does not exactly follow the changes in size, but individual variation in these complicated processes is to be expected).

NUMBER OF BODY-RINGS

It seems to be the rule that neither the total number of rings nor the number of abdominal leg-bearing rings is given in descriptions of North American Notostraca. There are few exceptions to this rule. Packard (1883) mentions the figures for one specimen of *Apus lucasanus* and Rosenberg (1947) quotes fixed figures characteristic of his species *A. oryzaphagus* and *A. biggsi*. The number of legless rings, on the other hand, is almost always recorded, and a slight variation in this respect is often noticed. Interesting information about *Lepidurus arcticus* is given, though only with some hesitation, by Chamberlin and Duncan (1924, p. 99): "The number of segments visible on the dorsal surface from the point of attachment of the carapace to the body seems to be either 26 or 27. . . . Behind the appendage bearing segments are five others, exclusive of the telson, which are without appendages of any sort." As the above-mentioned point of attachment stretches over the first body-ring, we may conclude that these authors found the number of body-rings to be 11+(11–12)+5=27–28 (telson not counted).

Even in descriptions of species from other parts of the world we seldom get information about the number of leg-bearing abdominal rings; at times a fixed total number is given, together with the number of legless rings, but without any attention to a possible variation of the former figure. Zaddach (1841) provides an exception; he says that in *A. cancriformis* the number of leg-bearing abdominal rings (in "pars abdominis posterior," according to Zaddach) is 17 or 18, the number of legless rings 5 or 6, and the total number of body rings always 34.

All authors except Chamberlin and Duncan seem to take it for granted that the species of Notostraca are nomomeristic, but this is not true of any of the species examined by me.

From figures 14 and 31 it can be seen that a variation in number is found not only in the legless rings, but in the leg-bearing ones, too. These varying numbers, together with the 11 thoracic rings, are combined in different ways to give a total number varying within the limits of a species. This is true of every species of which I have seen a reasonable number of specimens.

When I now proceed to analyze what I have found concerning the variation of these figures—a preliminary analysis in some respects because the material is rather scanty—I shall begin, not in the traditional way, with a treatment of the legless rings, but with the total number of rings and the number of abdominal leg-bearing rings. These are the primary characters. The number of legless rings is not a simple character; it is the result of the varying interplay of the two other series.

As for the total number of body-rings, the range of variation may be quite considerable in specimens from the same locality. In a new species of *Lepidurus* from Grand Coulee, Wash. (see p 39), the males have 30–33+i and the females 30+i–34 rings (fig. 14). The range is also great in *A. longicaudatus* from Wyoming (U.S.N.M. No. 58766), where the males have 41–44 and the females 39+i–43 rings (fig. 31). These are relatively extensive samples, the former containing 54 males and 42 females, the latter 33 males and 98 females. In smaller samples the range of variation is not so great. The extremely high and low numbers of rings in one sample are usually represented by rather few specimens.

No doubt the average number differs in various samples of the same species. But we cannot reasonably compare samples with 1, 2, or 10 specimens with samples containing a hundred or more specimens. Small samples give very uncertain figures, and museum work, in this respect, is much hampered by the fact that the great majority of samples contain a very small number of specimens. Statistical calculations, however desirable, are thus rendered very difficult.

There seems to be a general rule that species with a large number of rings have a greater range of variation than species with few rings, both in *Lepidurus* and in *Apus*. There are some exceptions to this rule, but not many, in the material I have seen. The fewest rings in *Apus* occur in forms that have a clear parthenogenetic tendency and that show a very small range of variation. About these more will be said later on (see p. 12). Similar forms belonging to a group with relatively few body-rings are found among species of *Lepidurus*.

Body-rings in the species of *Lepidurus* range from 25 to 34, those of *Apus* from 30 to 44. In the former genus, the high numbers of 30–34 are represented by two species only, *L. bilobatus* and a new species described in this paper, both of which differ from the other species of the genus in the number of leg-bearing abdominal rings, and, most evidently, in the number of legs. Apart from this grouping, and from what has been mentioned about parthenogenetic forms, I cannot find clear correlations between the number of rings and other characters. I doubt the validity of Rosenberg's (1947) method of distinguishing taxonomic units—and not lesser units at that, but species—by associating a certain number of rings with a certain size of specimen, because I think that further research is necessary to establish the conditions of the variation in size, which in some lots is considerable, in others rather small.

It is usual for the males to have a higher total number of rings than the females of the same species, though the rule has many exceptions.

It is, of course, necessary to know whether the number of rings is really fixed in adult specimens—non-adult stages are not considered here—or whether it increases with an increase in size of the specimen. I have attacked this problem, which has never before been investigated, in two ways: first by comparing the number of rings in small and large specimens in the same sample, and second, by comparing the old and the new integument of specimens in molting. All my observations agree that there is no general rule that larger specimens have a higher total number of rings than smaller ones. On the contrary, I have not infrequently found relatively small specimens with a high number (see fig. 14). Also, I have thoroughly examined about a hundred molting specimens of various species, and in none of them have I found a new ring appearing from the telson in the underlying, new integument. Judging from this, I think I am entitled to assume a fixed total number of rings in an adult specimen.

As for the variation in the number of leg-bearing rings, I have found no clear rule when comparing larger and smaller specimens from the same lot. When examining molting specimens, however, I have found two cases where the number of pairs of legs is increased by one in the underlying, new integument. Thus we must reckon with the possibility of an increase in the number of legs, and, consequently, even a slight increase in the number of abdominal leg-bearing rings, with an increase in the size of the animal. However, I think we can be sure that this increase, if present, will not be great.

The usual range in the number of leg-bearing abdominal rings in the genus *Lepidurus* is 9.5–13. This applies to all extra-American species I have examined (*L. apus*, *L. kirkii*, *L. viridis*), and to most American species (*L. arcticus*, *L. packardi*, *L. couesii*). This condition, together with the similarly small number of legless rings, at least in some cases helps to explain the short abdomen commonly mentioned as a character separating *Lepidurus* from *Apus*. Packard (1883), however, mentions that *L. bilobatus* has an unusually long abdomen, with many body-rings exposed behind the carapace; and I found, when examining a specimen of this species marked "type" in the U. S. National Museum, that it has 16.5 leg-bearing abdominal rings. Further, in material consisting of more than a hundred specimens of a new species from the State of Washington, I found this number to be 14.5–18, while 12 specimens of a variety of this species had 16–17.5. Corresponding to the high number of leg-bearing abdominal rings we have a higher total number of body-rings here than in other species of the genus; there are more legs, and, generally, more rings exposed behind the carapace. In my opinion, these figures indicate that there are two groups of species within the genus *Lepidurus*, whatever the taxonomic category we choose for them.

In the American forms of *Apus*, the number of leg-bearing abdominal rings ranges between 16 and 21 (males 16–18.5, females 17.5–21). In one large lot I have seen every number in this range represented (see fig. 31). Usually, the females have more, sometimes many more, leg-bearing abdominal rings than the males of the same species.

The variation in the number of legless rings is often used as a taxonomic character. This appears to be a useful character in South African forms of *Apus* (Barnard, 1929), but in the North American forms I have not found it to be of much aid in separating species. In *Lepidurus*, the number varies within narrow limits (4–5.5 in the great majority of forms), with no specific differences corresponding to the differences in number; a few specimens having 3, 3.5, or 6 legless rings show no other essential differences. There is, of course, the possibility that *L. packardi* may have a high number and that this character may be of taxonomic importance, the type specimen having 6 legless rings. But I do not think this is probable. In two lots (5 specimens) that I consider belonging to this species I found 4.5–6 legless rings.

In *Apus*, the whole range in the American specimens I have seen is 4.5+i–13 in the females and 8–15+i in the males. It seems that this range of variation ought to be great enough to include several species (or subspecies, or forms) with varying ranges, and I will certainly not deny the possibility that lower taxonomic units than species may be separated. However, I have seen a single lot of *Apus* that covered much of this range (9+i–13 in the females and 12.5–15+i in the males, as shown in table 6). This is an extreme example, the range of variation being smaller in other samples, especially in those with only a few specimens.

As a rule, the males have more legless rings than the females of the same species because they usually have fewer leg-bearing rings but a higher total number of rings.

BODY-RINGS IN PARTHENOGENETIC POPULATIONS

It seems rather remarkable that an author like Zaddach (1841), extremely careful in so many details, gives a fixed number of 34 body-rings in *Apus cancriformis*. And Rosenberg (1947) definitely states that all specimens, several hundred in number, of his species *A. oryzaphagus* have 35 body-rings (36 including the telson, according to him). I have seen 6 of them (U.S.N.M. No. 88360) and found 5 to have 35 and 1 to have 34+i body-rings. Rosenberg describes another form, under the name of *A. biggsi*, where all specimens have 36 rings (37 including the telson), but here it seems uncertain whether he had enough specimens for comparison. I found 3 of them having 36 and 1 having 35+i rings (U.S.N.M. No. 88361). In these cases the statements of a fixed number may result from the counting of incomplete rings as ordinary rings. Even so, the range of variation is very small. A significant observation is that these authors had only females in their samples.

Populations without males, or with very few, have been known for a long time. A list of such cases in *A. cancriformis* from Europe is given by Gaschott (1928, p. 276), from whose paper the following examples may be cited: Schulze examined more than 1,000 specimens during 4 successive years from the vicinity of Dresden, Germany, and found no males; Siebold (1871) found only females among about 9,000 specimens from Franken, Germany, collected during the summers of 1857–1869, in the last 6 of which he tried to examine the whole population; less extensive samples without males (100–243 specimens) are reported from Munich and Erlangen, Germany, Prague, Czechoslovakia, and Pavia, Italy. Further proof of the existence of parthenogenesis in this species is given by Grasser (1933, pp. 319–320), who succeeded in rearing specimens from eggs laid in aquaria populated by females only. These females were taken from a population where no males were observed. Bisexual populations of the same species are also common (Gaschott, 1928).

Obviously, there are similar conditions in the American species *A. longicaudatus*. *A. oryzaphagus* and *A. biggsi* (Rosenberg, 1947) are probably parthenogenetic populations, and, on account of significant similarities with *A. longicaudatus*, ought to be included in this species (p. 64). Bisexual populations seem to be more common in this species than in *A. cancriformis*, and in them the males sometimes are almost as well represented as the females. In such populations there is a greater range of variation in the total number of body-rings.

I have seen a number of relatively extensive samples of *Lepidurus arcticus*, *L. apus*, *A. cancriformis*, and *A. longicaudatus* with no males. Even here, the variation in the total number of rings is always small. The following sample, a lot of 113 females of *L. arcticus* from Ooglamie, Alaska (U.S.N.M. No. 7903), is representative (no males were found in the sample):

Number of specimens	Series of body-rings
2	11+10.5+4.5+i=26+i
12	11+11 +4.i =26+i
2	11+10.5+5.5 =27
85	11+11 +5 =27
12	11+11.5+4.5 =27

Among these specimens the incomplete rings varied in size from a tiny piece to an almost complete ring. No correspondence with size, or with other characters, was observed in any of the groups. The specimens varied much in size. We find, also, that 99 specimens have 27 rings and 14 specimens 26+i rings. This is the whole variation in the total number, a striking contrast to the conditions in bisexual populations. If we count the incomplete rings as counterparts of whole rings we might say that the population is nomomeristic. But I will not go so far as that. We cannot say for certain how the incomplete rings are to be interpreted. In any case, this analysis shows that we must consider these structures. If they had not been counted here we would have obtained a wrong impression of the variation.

In small lots, of course, we shall not infrequently find all specimens to have the same number of rings. The largest lot in which I observed this fact is from St. Paul Island, Pribilof Group, and contains 20 females, all having 27 body-rings. The number of specimens is, however, too small to enable us to draw any conclusion.

A few specimens of *L. arcticus* with 26 or 28 rings have been observed by me, but only in samples with males. These, like the majority of those without males, contain only very few specimens, as may be seen from the following lot of 14 specimens of *L. arcticus* from Cambridge Bay, Canada (U.S.N.M. No. 180638):

Number of specimens	Sex	Series of body-rings
1	♀	11+10 +5 =26
2	♀	11+10.5+4.5 =26
1	♀	11+11 +5 =27
8	♀	11+11.5+4.5 =27
1	♀	11+11.5+4.5+i=27+i
1	♂	11+11 +5 =27

Of *L. apus*, I have had access only to samples with few specimens. A representative example is the following lot of 17 females from Malma at Uppsala, Sweden (Uppsala Museum) (no males were found in the sample):

Number of specimens	Series of body-rings
1	11+12 +4+i=27+i
1	11+12.5+4.5 =28
13	11+12 +5 =28
2	11+13 +5 =29

Here we probably have a parthenogenetic population, because males of this species have never been found in Sweden. The range of variation is greater than in the sample of *L. arcticus* from Alaska, but it is interesting to notice the predominant representation of specimens with 28 rings, 14 out of 17 having this number. Of course, many more specimens must be examined to get an idea of the variation in this species.

Of *A. cancriformis*, only samples with few specimens have been accessible. One of these is the following lot of 33 females from the vicinity of Skara, Sweden (Uppsala Museum). (No males were found in the sample):

Number of specimens	Series of body-rings	
1	10+17 +5	=32
1	11+16. 5+5. 5	=33
26	11+17 +5	=33
1	11+17 +(sp. 2r.+3)	=31+sp. 2r.
2	11+17 +5+i	=33+i
1	11+17 +6	=34
1	11+18 +5+i	=34+i

Of this species, also, no males have been found in Sweden, so it is fair to assume that the population is parthenogenetic.

The first specimen of *A. cancriformis* listed, with only 10 thoracic rings, is abnormal, the ninth, tenth, and eleventh pairs of legs coming from the ninth and tenth body rings, an interesting deviation, as it shows that the anterior boundary of the polypody sometimes can be displaced farther forward than the eleventh ring (it is a common occurrence to see it displaced backward). But, in the present case, I think we had better leave this aberrant specimen out of consideration. The specimen with spiral growth may be counted as having 33 rings, because the two rounds of a spiral probably represent two rings. Thus we have 28 specimens with 33 rings, 2 with 33+i, 1 with 34, and 1 with 34+i rings, which means a quite considerable predominance of specimens with 33 rings. In several smaller samples this tendency is still more pronounced; one lot from the same locality comprised 17 specimens, all with 11+17+5=33 body-rings.

Now, in parthenogenetic populations we naturally expect to find a smaller variation than in bisexual ones, if hereditary characters are considered. Thus we can conclude that the number of rings is predominantly due to hereditary influences.

This conclusion will be strengthened when we consider the environmental conditions of Rosenberg's find of populations with a nearly fixed number of rings in the rice districts of California. These conditions are probably similar to those of the localities of the same species in Texas and Oklahoma. But in the latter localities we have a wide range of variation in the number of rings, and both sexes are represented in about equal numbers.

There is a temptation to regard *A. oryzaphagus* and *A. biggsi* as two clones, one characterized by 35 or 34+i and the other by 36 or 35+i rings. In *A. cancriformis*, there might be clones with 33 and with 34 rings. But such conclusions would be premature. There is still the possibility that the small variation existing in a parthenogenetic population is due to environmental influences.

In both *Lepidurus* and *Apus*, parthenogenetic populations are characterized by a relatively small number of rings. But there are bisexual forms, too, with a similar number.

It would be interesting to make comparisons with other groups of many-segmented Arthropoda where parthenogenesis is known to occur. In the Conchostraca we may expect something of this kind. Species with a varying number of rings are known in the Conchostraca Spinicaudata (Linder, 1945); and there is a species where a fixed number is postulated and probable, though not definitely proved, viz., *Cyclestheria hislopi* Baird. The latter has both parthenogenetical and bisexual propagation in the same population, changing its mode of propagation according to the time of year; in other Spinicaudata, where males often are very rare, parthenogenesis is likely to be found in many populations (as in *Limnadia*). Further investigations are highly desirable.

Conditions of a similar kind occur in the Diplopoda, where they are a little better known, but detailed comparisons may have to be postponed until we know more of the variation in the Notostraca. I wish to point out one feature, however, that was brought to my attention by Dr. Hans Lohmander: in the Diplopoda the parthenogenetic forms are known to become sexually mature when having a smaller number of rings than the bisexual ones. This reminds us of the fact that parthenogenetic forms in *Lepidurus* and *Apus* also have relatively few rings, although likewise having bisexual forms with just as few or even fewer rings. Matters seem to be rather complicated here.

It has been maintained by Gaschott (1928, p. 277) that males are relatively rare in cold districts and increase in number in warmer parts of the world. It is, of course, a striking observation that *Lepidurus arcticus* has very few males, or none at all, in many populations, and that males are known to be common in tropical species. The present material no doubt gives the impression that the principle is acceptable, though with the reservation that we still know rather little of the tropical notostracans. Rosenberg's find of parthenogenetic populations in such a warm locality as California's rice fields clearly shows that a cold climate is not necessary for the development of parthenogenesis.

GROUPING SPECIES BY NUMBER OF BODY-RINGS

To sum up some of the facts I have observed about the number of rings in species from all over the world, we get the distribution shown in table 3, p. 42, in which I have included the number of pairs of legs. The range of variation given in this table applies to the group of species as a whole, each species usually covering only a part of the whole range. Several species of both genera are missing because I have not yet been able to get specimens, but there is strong reason to believe that the missing species are merely synonyms of those recorded. Even some of the listed species are probably synonyms.

I have not seen any specimens of *Lepidurus patagonicus* Berg, but judging from the description (Berg, 1900) and redescription (Birabén, 1945) we may assume that it belongs, with *L. arcticus*, to the first group in table 3. The author says that it has 29 segments, 5 of which are apodous. Nothing is mentioned about variation or about number of legs. Only two specimens seem to be known, the later report of Bruch (1916) about a new locality being very uncertain because the illustration of a specimen (op. cit., fig. 1) clearly shows a form of the genus *Apus*. Thus *L. patagonicus* seems to be closely related to *L. packardi* and is perhaps identical with this species. It should be added that I regard all North American forms of *Apus*, and at least some of the South American ones, too, as belonging to the species *A. longicaudatus*, and *L. macrurus* as a synonym of *L. couesii*.

There are strong reasons to consider the groups of species in *Lepidurus* (see table 3) to be just as homogeneous and well demarcated from each other as genera usually are. Further, *A. cancriformis* is in important respects well distinguished from the other species of *Apus*. However, I think it best to postpone the taxonomic alterations thus implied until more is known about the number of body rings and legs, an extensive field of investigation that has only recently been brought to our attention.

EXPOSED BODY-RINGS

In most descriptions the number of exposed rings is mentioned and is often stressed as an important character. Very small differences in number have been given the value of a specific character, as when Lilljeborg (1877) says that *L. macrurus* has six to eight exposed rings and *L. couesii* only five, but Gurney (1923) says he does not think that too much importance should be attached to this. Sars (1901) and Barnard (1929) doubt the importance of the differences, because the varying influences of preservation cause an artificial variation in this respect. I agree with them that this is obviously often the case (see p. 5).

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In samples of unusually well-preserved specimens I have observed a great range of variation in the number of exposed rings, particularly in *L. couesii* (2–8), in the new species of *Lepidurus* (10–19), and in *A. longicaudatus* (20–26). No correlation with other characters is noticed in these samples, with the exception that specimens with many exposed rings in most cases have longer rings than those with fewer exposed but with a carapace of about the same size. The appearance of the rings supports the idea that the variations are due to contraction.

Nevertheless, we must not altogether overlook this character. By their large number of exposed rings, *Lepidurus bilobatus* and the new species of *Lepidurus* (pls. 2, 3, and 4) are distinguished from the other species of the genus (though *L. arcticus*, too, sometimes may have a rather large number, as may be seen on plate 1), and suggest the genus *Apus*. It is quite a conspicuous character, and one that is easily explained by the great number of abdominal rings in these species. However, the variety of the new species described in this paper has just as many abdominal rings as do these forms, but only 7 to 10 exposed rings as against 10 to 19. Here the posterior emargination of the carapace is not nearly so deep as in the typical form, and this is certainly part of the explanation. However, the difference in number seems a little too great to be explained by this fact alone. One is tempted to say that the carapace is, relatively, a little larger here than in the typical form. Measurements confirm this; not only is it larger in relation to the total length but also in relation to length or width of separate body-rings. The body-rings are set just as closely together in the principal form as in the variety, and thus there appears to be a real difference in the relation between the length of carapace and of body in the two forms.

We see from the above that the number of exposed rings is not a simple character, but is the result of the combined action of several separate features, one of which is subject to variation caused by artificial means. Considerable caution is necessary when dealing with this as a taxonomic character.

The same thing may be said about the length of the carapace in relation to the length of the exposed part of the body. Packard (1883), when separating his species within the genus *Apus*, makes extensive use of this character. Because of the considerations noted, I do not think it advisable to pay much attention to this feature.

SIZE AND ARMATURE OF THE BODY-RINGS

As we have seen, the lengths of the individual body-rings, though not used as a separate character, influence two that are commonly used: the number of exposed body-rings, and the length of the carapace in relation to the total body length. It should be made clear, too, that these measurements are not easily determined with reasonable accuracy. They increase, of course, with increasing age, but to a degree that certainly varies.

The shape of the spines near the caudal border of the rings is rather uniform in each of the North American species. Accessory small spines sometimes occur on the ventral side of the legless rings, but this does not seem to be a specific character. In several species of *Lepidurus*, the ventral spines on the hind margin of the legless rings are smaller than the lateral and dorsal ones. The number of these

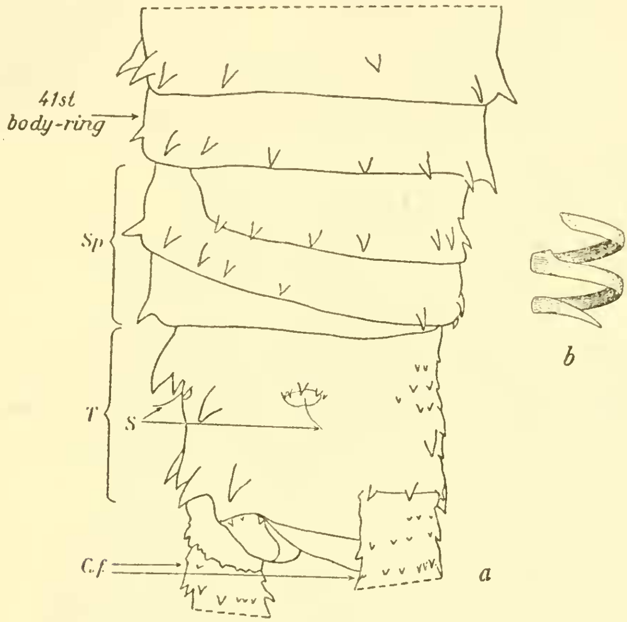

FIGURE 3.—*a*, Dorsolateral view of distal portion of abdomen of a male of *Apus longicaudatus* LeConte (U.S.N.M. No. 11602, type of *A. lucasanus* Packard) showing a right-handed spiral of a little more than two rounds, beginning in the middorsal line and evenly tapering at distal end, × 29. (*Sp*, spiral; *T*, telson; *S*, dorsal sensory setae; *C.f.*, caudal filaments.) *b*, Schematic drawing of the spiral.

spines, and of the other ones, too, is subject to considerable individual variation. Even in *Apus* the number of spines on each ring will not do as a specific character, though it is more constant in some lots than in others. Caution certainly is needed in dealing with this character, frequently used and much overrated in old descriptions.

INCOMPLETE BODY-RINGS

Barnard (1929, p. 232) seems to be the only author who has paid any attention to the interesting subject of incomplete body-rings. He states: "The interpolation of an incomplete segment immediately

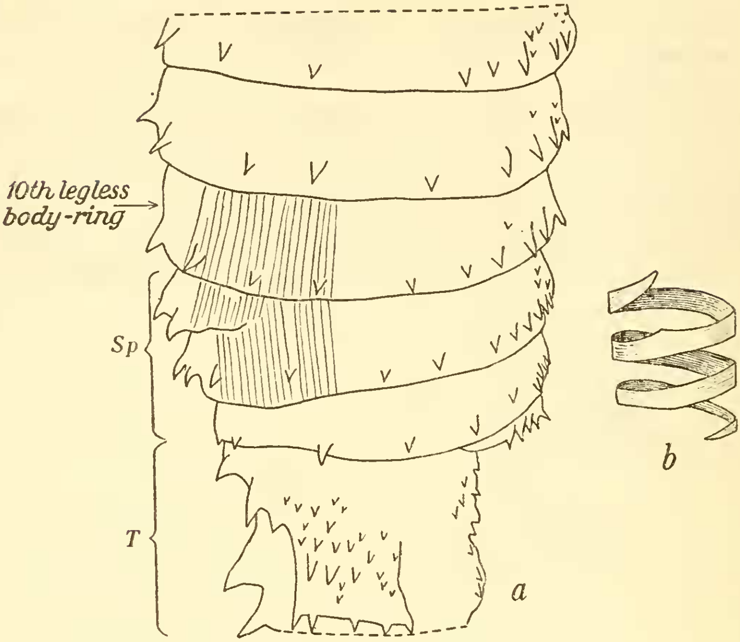

FIGURE 4.—*a*, Lateral view of portions of the abdomen and telson of a male of *Apus longicaudatus* LeConte (U.S.N.M. No. 11604) showing a left-handed spiral of about two and three-quarters rounds, beginning dorsolaterally and evenly tapering at distal end, × 28. Arrangement of muscle bundles indicated on the left side. (*Sp*, spiral; *T*, telson.) *b*, Schematic drawing of the spiral.

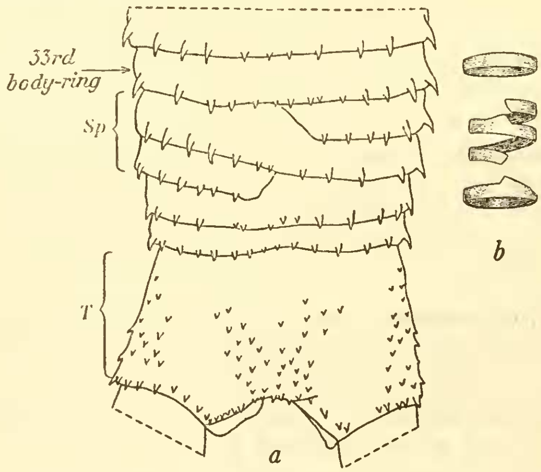

FIGURE 5.—*a*, Ventral view of portions of the abdomen and telson of a female of *Apus longicaudatus* LeConte (U.S.N.M. No. 82034) showing a right-handed spiral of two rounds placed within the series of normal rings and beginning and ending in the mid-ventral line, × 29. (*Sp*, spiral; *T*, telson.) *b*, Schematic drawing of the spiral and the rings immediately anterior and posterior to it.

preceding the telson occurs fairly often. This incomplete segment is visible on one or the other side, or only on the dorsal surface." He does not count it when giving the number of rings. Incomplete body-rings occur frequently; in one lot of the new species of *Lepidurus* described herein, for example, 10 out of 54 males and 7 out of 42 females show this structure in varying degrees of development. Nearly half the specimens in a lot of *A. longicaudatus* have incomplete rings: 14 out of 33 males, and 44 out of 98 females (fig. 31). These examples show that it is best not to omit them when counting the rings. They occur at any place around the front boundary of the telson (I have found, in two cases only, a piece of an incomplete ring in the middle of the series of abdominal rings) and may be of any size from a tiny piece to an almost but not quite complete ring. Two or even three of them may occur in the same specimen (fig. 16). Under their integument there is always a continuation of the longitudinal

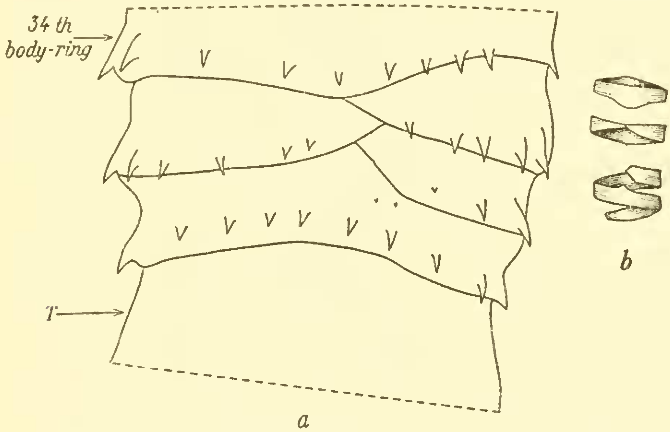

FIGURE 6.—*a*, Ventral view of portions of the abdomen and telson of a female of *Apus longicaudatus* LeConte (U.S.N.M. No. 18908) showing a right-handed spiral of a little more than one and one-half rounds, beginning in the midventral line, and preceded by a one-round structure similar to a spiral, × 29. (*T*, telson.) *b*, Schematic drawing.

muscles. I cannot say, as yet, whether such a piece sometimes grows to be a complete ring. The existence of a piece of an incomplete ring within the series of abdominal rings shows that they do not necessarily become complete rings and that they may be followed by a normal ring caudally.

SPIRAL GROWTH

Occasionally the regular growth is disturbed, and the rings in some part of the body are replaced by a real spiral (Linder, 1947). In more than 2,000 North American specimens I have found 15 cases of this, some of which are illustrated in figures 3 through 7, 17, and plate 7, figures 1 and 2. Most often the spiral ends at the front of the telson, but sometimes it appears in the midst of the series of abdominal rings, with normal rings following it caudally. There may be two spirals in one specimen (fig. 7 and pl. 7, figs. 1, 2), and they may be right-handed or left-handed. The largest spiral I have seen, consisting of a little more than 4 complete turns, was observed in a large female of the new species of *Lepidurus* (fig. 17), one of the two cases where the spiral was found to affect the leg-bearing part of the abdomen. It forms the whole legless part of the body, too. A spiral usually begins in the

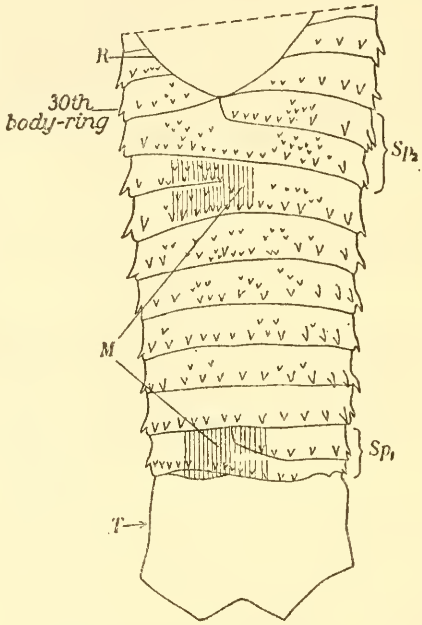

FIGURE 7.—Ventral view of abdomen of a female of *Apus granarius* (Lucas) from China (Stockholm Mus.) showing two right-handed spirals in the same specimen, both beginning in the midventral line, the anterior one (Sp_2) of two rounds and ending openly at the midventral line, the posterior one (Sp_1) of a little more than one and one-half rounds and with the distal end evenly tapering, × 14. (*M*, muscle bundles indicated in part of the body to show that their courses are not influenced by the spirals; *R*, ridge bordering the leg-bearing area; Sp_1, Sp_2, spirals; *T*, telson.)

midventral or middorsal line, but in one case (fig. 4) it begins dorsolaterally. The end of the spiral may be found in any place around the periphery of the anterior margin of the telson and is often tapered continuously for a rather considerable distance. If the spiral occurs within the series of normal rings, it ends only midventrally or middorsally, in the cases which I have seen, and no long tapering has been observed.

Though the occurrence of spiral growth and of incomplete body-rings has no significance at all for the taxonomy of the Notostraca, I think that both these kinds of abnormalities are of considerable interest, and I hope that others who come across cases of spiral growth will publish their findings.

THE TELSON AND SUPRA-ANAL PLATE

The telson is heavily chitinized and is thus very little subject to the influence of the preservation fluid. Disregarding the supra-anal plate, the telson is very short in *L. couesii* and *L. packardi*, and unusually long in the new species and variety of *Lepidurus* (figs. 9, 10,

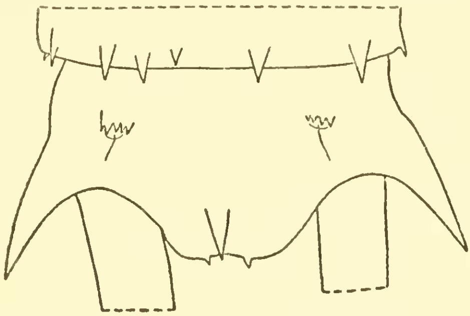

FIGURE 8.—Dorsal view of telson of a female of *Apus cancriformis* (Bosc) from Safi, French Morocco (U.S.N.M.), × 23.

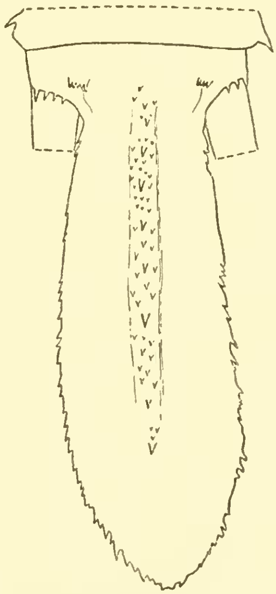

FIGURE 9.—Dorsal view of telson of a male of *Lepidurus couesii* Packard (Stockholm Mus.), × 13.

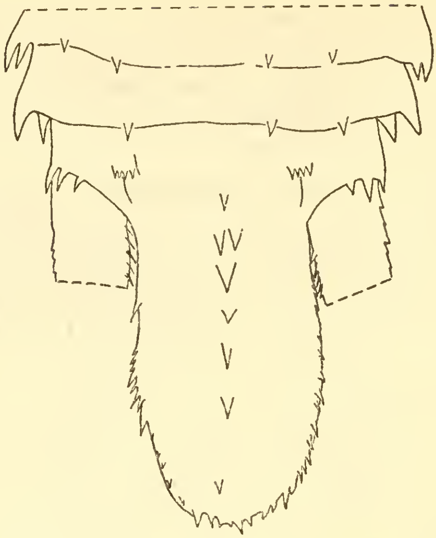

FIGURE 10.—Dorsal view of telson and last two body rings of female holotype of *Lepidurus packardi* Simon (Paris Mus.), × 19.5.

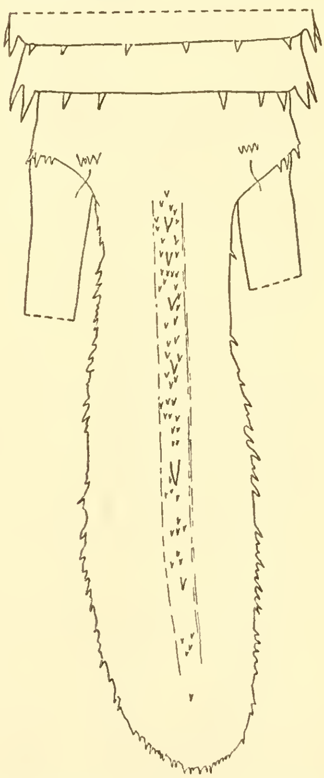

FIGURE 11.—Dorsal view of telson and last two body-rings of a female of *Lepidurus couesii* Packard from Jenissejsk (Stockholm Mus.; labeled *L. macrurus* by Lilljeborg), × 13.

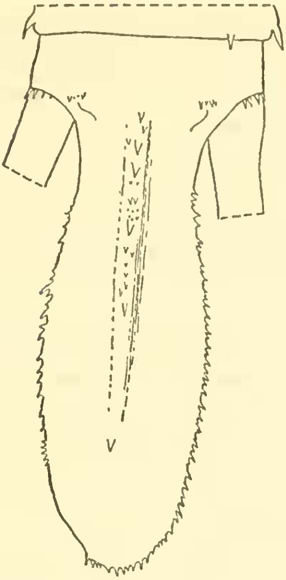

Figure 12.—Dorsal view of telson of a female cotype of *Lepidurus couesii* Packard (U.S.N.M. No. 11605), × 13.

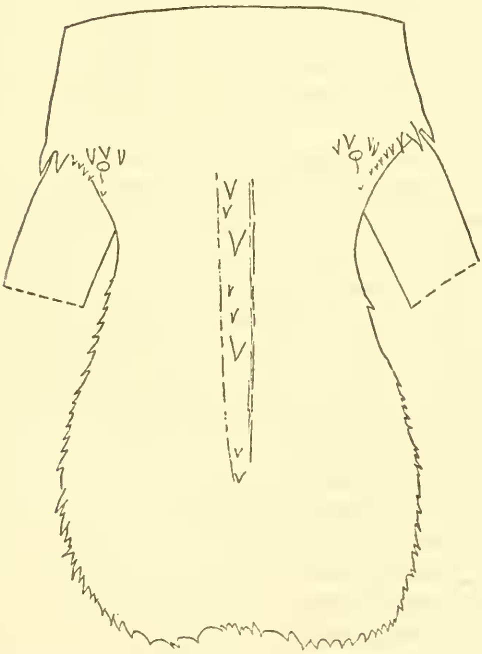

Figure 13.—Dorsal view of telson of a female of *Lepidurus bilobatus* Packard, from Utah (U.S.N.M. No. 11606; labeled "type"), × 20.

and 28). Its proportions do not vary much individually, at least not in the species of *Lepidurus*, and are well worth using as a taxonomic character, though they do not always separate species as well as in the case just mentioned.

The presence of a supra-anal plate has for a long time been the main character of the genus *Lepidurus*. Sometimes we meet forms of *Apus* (see fig. 8, and also Gauthier, 1934, pl. 2, fig. D) which show the appearance of such a plate not much smaller than that in some specimens of *L. arcticus*. However, for practical purposes the character seems to be quite acceptable.

The supra-anal plate has always been regarded as a useful taxonomic feature, and this course seems to be justified, provided we do not pay too much attention to its form. Holmes (1894, p. 586) has an extreme example of variation in this respect in a lot of only 5 specimens of *Lepidurus lemmoni*, in which it "may be rounded, truncated (obliquely so in some specimens), or, in some cases, bilobed." Bilobation of this plate is not a valid character. Sars (1896) figures such a condition in some specimens of *L. arcticus*, and Spandl (1925) the beginning of a bilobation in the European species *L. apus*. In the new species of *Lepidurus* from the State of Washington, I have observed varying bilobation, or none, in specimens of both sexes and of all sizes (figs. 15 and 24). Having found in several cases a variation in this respect within the limits of a species, I cannot, of course, follow Sidorov (1927) when he uses the bilobation as a generic character.

The largest supra-anal plate among all Notostraca is found in males of *L. couesii*, where its length can approach 44 percent of the length of the carapace (fig. 11). In *L. arcticus*, on the other hand, it is unusually small, being 7 to 13 percent of the length of the carapace.

The spines on the dorsal side of the supra-anal plate are sometimes valid characters, though their number is not fixed for each species but varies within certain limits. I have noticed 0–4 of them in *L. arcticus*, 4–19 in *L. packardi*, and 2–7 in the new species of *Lepidurus*. In these species they always occur in a reasonably straight row, but not on a keel, and they are rather similar in size. The two remaining North American species of *Lepidurus* are very different in this respect. In *L. couesii* there is a strong middorsal keel covered with very numerous spines (20–100) that vary considerably in size (figs. 9 and 11), most of which are very small and in this respect are similar to what I have called accessory small spines sometimes occurring on the ventral side of the legless body-rings in several species (p. 19). A varying number reach a size comparable with that found in other species of the genus, though not quite so large, and there are intermediate sizes, too. *L. bilobatus*, of which I have seen only a few specimens, has a supra-anal plate similar to that of *L. couesii*, though the keel is less well marked and the spines are fewer, 4–6 large ones and a trifling number of small ones (see fig. 13).

In *L. couesii*, the number of spines on the supra-anal plate obviously increases with the size of the animal, but in other species I cannot say that this is the rule.

The spines around the dorsal sensory setae and around the bases of the caudal filaments usually do not present valid characters in American forms, and as for the conspicuous spines placed more middorsally on the telson in the genus *Apus*, they vary in number in almost every sample. Later on (p. 59), I will give examples of this that may go to show that the number is not a reliable character. This variation also occurs in several extra-American species of *Apus* such as *A. numidicus* (Barnard, 1929, p. 234), *A. granarius*, and *A. australiensis*. The caudal filaments present good sexual characters in the armature of their basal parts (Gurney, 1924, 1925), because those of the female are bristly and those of the male armed, at least at the base, with rounded knobs. This, however, seems to apply to forms of *Apus* only. In other respects I have not found these filaments useful for taxonomic purposes.

THE CARAPACE

The carapace is more flattened in the male than in the female. The relation of its width to its length is, according to Barnard (1929), a valid character in some South African species of *Apus* (though not in all of them!). I have given this relation in the descriptions, but, at least in *Apus*, I have found no conspicuous differences in the American material. Many spines, which sometimes are very small, often occur in both genera on the dorsal surface, especially on the carina. The presence, absence, or number of these structures cannot, as it would seem, be used as a taxonomic character; many times I have found in a single lot great variation in this respect, without any correlation with other characters. Barnard (1929) found similar variation in South African material of *Apus* and he, too, rejects its taxonomic importance. The lateral margin of the carapace is regularly furnished with some very small spines, at least in its posterior part, and in the variety of the new species of *Lepidurus* described here, these spines are large and conspicuous around most of the margin (pl. 5, fig. 1). As for the posterior emargination of the carapace, early authors used to pay a great deal of attention to the number of spines found on it, and this character still appears in descriptions, sometimes with pretensions of separating species. However, Braem (1893) and many authors after him have found a great range of variation in this respect in many species, and so have I in the American material. On the other hand, the size and pattern of these spines in several cases may prove helpful to the taxonomist. In most forms the spines are fairly equal in size and regularly placed, but sometimes (in *L. packardi* and *L. bilobatus*) there are large spines interspersed between much smaller ones at fairly regular intervals, and this seems to be worth considering in the taxonomy, because the individual variation in this respect is very slight in the material I have examined. The depth of the posterior margination is also worth attention.

On the ventral side, just in front of the antennae, we find the supra-antennal crest. Simon (1886) attaches some importance to the appearance of this crest, which in some forms is quite smooth and in others is furnished with small tubercles or is almost serrated. As a taxonomic character, this seems to be well worth attention.

THE NUCHAL ORGAN

Barnard (1929) found that the height and location of the tubercle on which the nuchal organ is placed were very useful in distinguishing the South African species of *Apus*. The North American forms of the genus, however, are uniform in this respect. In *Lepidurus*, I have not observed any considerable differences in the height of it, and in almost all species its location is more or less uniform, that is, it occurs somewhat between the hind part of the eye-tubercles (fig. 19 and pl. 7, figs. 3–6). Aberrant in this respect is the new species from Washington, in which it occurs considerably behind the eye tubercles. The fact that the eyes are unusually small in this species may have some bearing on this, however. The same conditions occur in the variety of this species. According to Holmes (1894), the nuchal organ in *L. lemmoni* is "located considerably behind the posterior margin of the eyes." As the posterior margin of the eyes is situated in front of the posterior margin of the eye-tubercles, we cannot say for certain whether the organ is placed behind the latter margin or not.

THE SECOND MAXILLAE

Sars (1901) observed that the second maxillae are relatively larger in *Lepidurus* than in *Apus*, though "the exopodal part" may be much larger in *Apus*. What he calls "the exopodal part" is only the free end of the efferent duct of the maxillary gland. This is called "palpus" by Wolf (1911, p. 260), who made another important observation: "Vielleicht dürfte auch das von mir an vielen Arten beobachtete Unterscheidungsmerkmal allgemeine Geltung haben, dass nämlich bei Lepidurus die 2. Maxille seitlich einen Palpus trägt, während bei den Triops-Arten dieselbe vollständig rudimentär geworden, und der bedeutend vergrösserte Palpus frei zu stehen scheint." A similar reduction is mentioned by me in an earlier paper (1945, p. 13). I can now confirm that in most species of *Apus* (*A. australiensis*, *A. granarius*, *A. numidicus*, and *A. longicaudatus*) middle-sized and large specimens have only the free end of the efferent duct of the maxillary gland remaining. In small specimens of these species the reduction has not gone so far as that, the maxillae being similar to those of *Lepidurus*, but relatively smaller and pushed laterally, so that the median spines of the two limbs cannot possibly meet each other in the midline. In *A. cancriformis*, however, we find an exception. Here, as in the various forms of *Lepidurus*, I have observed no dwindling of these limbs in large specimens.

It remains a question whether or not the free end of the duct from the maxillary gland should be regarded as a constituent part of the maxilla. The above-mentioned authors obviously consider it a part of the limb, as do Cannon and Leak (1933).

It is easily observed that there is no intimate coalescence between the two parts in the Notostraca. In the Conchostraca, too, they are clearly separated from each other. From a theoretical point of view this seems peculiar, and may, of course, be taken as a secondary change. Claus (1873), however, says that the free end grows, in early post-embryonal stages of *A. cancriformis*, in a place clearly apart from "the masticatory part," and later comes closer to it. He gives his statement with some hesitation, but, so far as I can see, no one has since been able to verify or contradict it.

Grasser (1933) reveals many facts about the development of the excretory organs in early stages of *A. cancriformis*, but gives no clear information on this point, saying (p. 349): "Der Ausführzapfen . . . erhebt sich zu gleicher Höhe wie die . . . Anlagen des Maxillen—und des ersten Thorakalgliedpaares." Further examination of very young stages seems desirable.

THE LEGS

I have not paid much attention to variations of the proportions of the endites of the first pair of legs, because I have found, as did Barnard (1929), that individual variation is great in this respect. Nor have I measured the length or width of the stem, for similar reasons. In other respects the legs of various species are known to be very similar to each other, though it has been known for a long time that, as a rule, the endites of the first legs are longer in *Apus* than in *Lepidurus*. Perhaps we might be able to find some distinguishing characters in the structure of the endopodites of the first pair of legs, which are furnished with setae in some forms and without setae in others, and also, perhaps, in the preepipodites. However, the age variation in these respects is not yet known. Sometimes the epipodites and the exopodites are very much swollen, thus giving the legs a peculiar appearance, but, as the variation shows, this has no taxonomic significance.

The number of pairs of legs is seldom given in descriptions of notostracans. They are regarded as extremely difficult to count. I admit the difficulty, though with a pair of fine needles and a good binocular microscope the task is not at all impossible. Some training however, is highly advisable if one wants to get an accurate result with a minimum of effort.

When the number is actually mentioned in the literature, it appears that only one or two specimens have been counted, and a fixed number is given for each species. I have found only one exception to this: Chamberlin and Duncan (1924) noticed a variation in the number of leg-bearing rings (p. 9) and also mentioned that the number of pairs of legs in *L. arcticus* is 41–46.

In fact, the number is not constant in any of the species of which I have examined a reasonable number of specimens, though it seems to be fairly constant in parthenogenetic populations. The American species present the following figures: *L. arcticus* 41–46, *L. packardi* (1 specimen) about 35, *L. couesii* 35–40, *L. lemmoni* unknown, *L. bilobatus* (1 specimen) about 62, the new species of *Lepidurus* 60–71, the new variety of *Lepidurus* 67–68 (2 specimens), and *A. longicaudatus* 54–66. In two of the above species approximate figures are given because the specimens in question were not in a sufficiently good state of preservation to allow an accurate counting of the legs without causing some damage to the specimens, and, the specimens being unique, dissection did not seem advisable. In some species, at least, the females usually have a few more legs than the males.

We notice that the greatest number of legs is found not in *Apus*, where the leg-bearing abdominal rings may be as many as 21, but in a species of *Lepidurus*, where these rings do not number more than 18. Within the latter genus, however, all species with 14.5–18 leg-bearing rings have 60–71 pairs of legs, and the species with 9.5–13 leg-bearing rings have only 35–46 pairs. For counts of extra-American species, I refer readers to table 3, in which some small changes may be necessary when more specimens are counted.

It seems clear that the number of legs is a taxonomic character of no small importance in many cases, and that we have to take the trouble to count them.

NORTH AMERICAN SPECIES

Genus **LEPIDURUS** Leach

Lepidurus Leach, 1816, p. 259.—Simon, 1886, p. 428 (earlier synonymy).
Bilobus Sidorov, 1924; 1927.

The main character of the genus is the presence of a supra-anal plate on the telson, and this seems to be a reasonably good character for practical purposes (p. 26). Further, the first pair of legs have comparatively short endites, not much projecting beyond the margin of the carapace (in the new species from Washington, however, they are quite long), the legless rings are 3–8, mostly 4–6 in number, and the ova are reported as larger than in *Apus*.

The second maxillae are well developed, not reduced in size or absent as in most species of *Apus*.

It is often stressed that, in relation to the body, the carapace is larger than in *Apus*, thus leaving a smaller number of body-rings uncovered. This certainly is true of most species, but in *L. bilobatus* and the new species the number of such rings is quite as great as the usual number in *Apus*.

In the generic diagnosis we should include the numbers of body-rings and of pairs of legs. In these respects, there are two groups of species in the genus. *L. apus*, *L. arcticus*, *L. couesii*, *L. kirkii*, *L. packardi*, and *L. viridis* are characterized by fewer rings and legs: 9.5–13 abdominal leg-bearing body-rings, 25–29 body-rings in all, and 35–46 pairs of legs. The second group consists of *L. bilobatus* and the new species and variety of this genus. Here we find 14.5–18 abdominal leg-bearing body-rings, 30–34 body-rings in all, and 60–71 pairs of legs. These differences may be expressed by saying that the leg-bearing part of the abdomen is more developed in the last group than in that first mentioned.

This is not the place to give a world-wide enumeration of the species of *Lepidurus* described by various authors, or to give an account of their synonymy, but, as far as I can see, so many of these are synonyms only that I can maintain that I have examined specimens of all species except *L. patagonicus*, and that the above considerations apply to all species of the genus I have examined.

Sidorov (1927) refers to his paper (1924) in which he erects a new genus, *Bilobus*, for *L. bilobatus*. This genus is founded on minor characters, some of which are not even fit for specific demarcation (bilobation of the supra-anal plate, for example, is observed in many species). The 1924 paper, written in Russian, was not available for my inspection.

As for other characters, readers are referred to the descriptions in this paper.

About the distribution, I agree with Barnard (1929, p. 228): "*Lepidurus* is confined to the more boreal portions of the Palaearctic and Nearctic regions, New Zealand, Tasmania, the southwestern and southeastern coastal belts of Australia, and Patagonia. In regions of a hotter and more arid climate, subject to periodical droughts, it is replaced by *Apus*. The limits of distribution of the two genera overlap in places, but in general the above marked separation holds good."

In North America, members of the genus occur in the Arctic and in the western part of the continent: *L. arcticus* in northern Canada, Greenland, and Alaska; and the other species in Alberta and Saskatchewan, in Canada; and in Washington, Oregon, Montana, Idaho, North Dakota, California, Utah, Nevada, Arizona, and Colorado, in the United States. East of the Mississippi, *Lepidurus* is not recorded and east of the Missouri only once (Max, N. Dak.). It is, of course, possible that these animals really do not live in that area, but perhaps it would be premature to regard this as an established fact. We must not forget that notostracans are very easy to overlook even in places where much general collecting is done, and *Lepidurus* is found in other parts of the world, such as southeastern Australia and New Zealand, where the climatic conditions are similar to those in the eastern United States. The western part of North America, from Alberta in the north to Arizona in the south, in spite of the relative smallness of the area, and the comparatively few localities from which material is reported, presents a richness of forms unparalleled in other parts of the world. Four species are found here as against two in boreal Europe and Asia, one or possibly two (others are certainly synonyms only) in Australia, and one in South America. Species with a large number of leg-bearing rings (*L. bilobatus* and the new species of *Lepidurus*) have not been found anywhere else in the world.

It has been advanced that there is a biological difference between *Lepidurus* and *Apus*, the latter occurring in pools which regularly dry up, while the former are found in permanent waters (Brauer, 1878, and Barnard, 1929). However, I have observed *L. apus* in several ponds in Sweden which dry up every year. Further, Brauer states (p. 587) that species of both genera sometimes live in the same pool. Perhaps the eggs of *Lepidurus* may be able to stand some desiccation, though those of *Apus* certainly can stand more, or perhaps the different species of *Lepidurus* have varying abilities in this respect.

Both *Lepidurus* and *Apus* are recorded from Montana, Oregon, California, Nevada, Utah, Colorado, and Arizona, though they are not known to occur together in the same pool there. It is not known what differences there may be between the respective localities.

KEY TO THE NORTH AMERICAN SPECIES OF LEPIDURUS

A. Leg-bearing abdominal rings 9.5–13, inclusive, front part of nuchal organ between hind part of eye-tubercles, not far from hind margin of eyes.
  - *a.* Endites 3–5 of first leg rather similar in size, very little or not at all projecting beyond margin of carapace.............. **arcticus** (p. 33)
  - *b.* Endites 3–5 of first leg much dissimilar in size, fifth endite of first leg clearly projecting beyond margin of carapace.
    1. Mediodorsal spines on supra-anal plate not on a keel, few in number, rather similar in size.............................. **packardi** (p. 33)
    2. Mediodorsal spines on supra-anal plate on a distinct keel, numerous (20–100), and highly variable in size............... **couesii** (p. 34)

B. Leg-bearing abdominal rings 14.5–18, inclusive.
  - I. Front part of nuchal organ between hind parts of eye-tubercles, not far from hind margin of eyes......................... **bilobatus** (p. 38)
  - II. Nuchal organ considerably behind eye-tubercles.
    - *a.* Hind part of lateral margin of carapace with minute spines. **lynchi** (p. 39)
    - *b.* Hind part of lateral margin of carapace with large spines, directed straight outward................. **lynchi var. echinatus** (p. 49)

L. lemmoni Holmes (p. 50) is regarded as insufficiently known to be included in the key.

LEPIDURUS ARCTICUS (Pallas)

PLATE 1 (FIGURE 1)

Monoculus arcticus PALLAS, 1793, pp. 39, 679.
Lepidurus glacialis PACKARD, 1883, p. 316.—SARS, 1896, p. 68, pls. 11–13.—CHAMBERLIN and DUNCAN, 1924, p. 101.
Lepidurus arcticus JOHANSEN, 1922, p. 4.—LINDER, 1932, p. 192.

Description.—For a detailed description readers are referred to Sars (1896). So far as I can see, there are no essential differences in structure between American and European or Asiatic specimens. Simon (1886, p. 429) says, "Lamina analis parva attenuata brevior quam telson (in speciminibus sibiricus) vel parum longior (in sp. americanis)," but he probably had too little material to cover the individual variations; in the extensive material I have seen I cannot find such a difference. Sømme (1934) noticed varying sizes of the spines on the dorsal side of the legless body-rings in specimens from various European localities, but it is uncertain whether these dissimilarities lie within the range of individual variation or characterize geographical races. In any case, I do not think they can be given specific value.

The number of body-rings is 11+(10–12)+(4–5)=26–28, and the number of legs is 41–46. Length of supra-anal plate is 7–13 percent of length of carapace.

Localities.—The localities in the collection of the U. S. National Museum are recorded by Johansen (1922).

Distribution.—For distribution, see Linder (1932).

LEPIDURUS PACKARDI Simon

FIGURES 10, 19, *a*; PLATES 2 (FIGURES 1, 2) AND 7 (FIGURE 6)

Lepidurus packardi SIMON, 1886, p. 448.

Description.—The principal points of the description are as follows: Carapace broadly oval, carina conspicuous in posterior third but disappearing anteriorly, posterior emargination with minute, numerous spines interspersed with slightly larger ones at regular intervals (8–9 on each side). Nuchal organ small, broadly oval. Abdomen short, hardly projecting behind carapace. Abdominal legless body-rings with 8 strong, sharp spines dorsally and 20–25 smaller ones ventrally. Supra-anal plate small, with parallel sides and rounded apex, and with 8 spines in the dorsal middle line. Endites 2, 3, and 4 of first leg rather thick and flattened and projecting beyond the margin of the carapace, endite 5 projecting beyond first third of carapace. Length of carapace 15.5 mm., width 14 mm.

Type locality.—California.

Type.—Type in Muséum d'Histoire Naturelle, Paris. Thanks to the courtesy of Dr. Marc André, of the Muséum d'Histoire Naturelle, I have had an opportunity to examine the type. The species does not seem to have been mentioned in the literature after its establishment, and a few supplementary notes about some details of its structure may be desirable. There is only one type, a female; number of body-rings: 11+10+6=27; telson (supra-anal plate not considered) very short; length of supra-anal plate 20 percent of length of carapace; width of carapace, as measured from the carina to both sides, 7.5+7.5 mm; nuchal organ oval, not so high as eye-tubercles, and placed between their hind parts, so that only a very small part of it reaches farther posteriorly than these; about 35 pairs of legs.

Localities.—I have examined a male and two females from Davis, Calif. (U.S.N.M. No. 82030), and a male and female from Lassen County, Calif. (U.S.N.M. No. 9377).

This species is not known from places other than those mentioned.

Remarks.—I have placed in this species some California specimens which belong to the group with 9.5–13 leg-bearing abdominal rings and which certainly are not *L. arcticus*, *L. couesii*, or *L. lemmoni*. Particulars are given in table 1. They agree well with *L. packardi* in the armature of spines on the posterior emargination of the carapace, and in having only large spines on the supra-anal plate. On the other hand, most of them have more spines on the supra-anal plate than the type specimen, and fewer teeth on the last legless ring, but, in these respects, individual variations may be expected. It is to be added that *L. patagonicus* Berg from South America (p. 17) obviously is nearly related to this species and possibly identical with it.

LEPIDURUS COUESII Packard

FIGURES 9; 11; 12; 19, *b*; PLATES 1 (FIGURES 2, 3) AND 7 (FIGURE 5)

Lepidurus couesii PACKARD, 1875, p. 311; 1883, p. 317.—JOHANSEN, 1921, p. 29.
Lepidurus macrurus LILLJEBORG, 1877, p. 9.—SIMON, 1886, pp. 429, 448.—SARS, 1897, p. 464; 1901, p. 143.

Description.—I have examined two males and one female, marked "type" (U.S.N.M. No. 11605). According to the label, they were collected in Montana by E. Coues, as were Packard's type specimens, and I think there is no doubt about their being true types. Further, I have seen two males from Montana in the Stockholm Natural History Museum that were sent from Packard and thus, with some justification, ought to be regarded as types, too.

It appears from these specimens and from seven others from North America (table 1) that *L. couesii* is easily distinguished from other North American species of the genus. The number of rings is 11+(9.5–11.5)+(4–5.5)=25–27. The nuchal organ has its front part placed between the hind part of the eye-tubercles. The supra-antennal crest is quite smooth.

It is often mentioned as a good character of this species that the supra-anal plate is unusually long. This certainly is true of the males, where it can reach a length of 40–42 percent of the length of the carapace (in type specimens), thus by far exceeding the length in any other species of *Lepidurus* I have examined. In the females, however, we find quite an ordinary length of this plate to be 17–29 percent of that of the carapace. A reliable character, for both sexes, is that the supra-anal plate has a distinct keel middorsally, furnished with a large number of spines (from 20 up to more than a hundred). Most of these spines are minute, much smaller than in other species, but there are also larger ones interspersed at varying intervals, and intermediate sizes occur, too. However, the largest spines do not quite reach the size usual in other species. Another conspicuous character is the shortness of the telson. Its length, disregarding the supra-anal plate, is less than half of its width.

Packard (1883, p. 317) says about the spines on the posterior emargination of the carapace that they show a tendency to become obsolete on the lower part of the emargination, and that they are finer than in "the European species." I confirm this. They have a rather worn appearance, though variations occur.

So far as I can see, the number of pairs of legs is not given by earlier authors. I have found it to be 35 to 40.

For other particulars, see table 1.

Localities.—The following American localities are represented in the material examined by me: Montana, 2♂ and 1♀ (cotypes), U.S.N.M. No. 11605; 2♂ (cotypes), Stockholm Museum. Idaho, 25 miles north of Ashton, 2♂ and 2♀ (U.S.N.M. No. 55800); "Idaho," with no particulars, 1 specimen, badly preserved (U.S.N.M. No. 50569). Max, N. Dak., 1♀ (U.S.N.M. No. 67699). Rocky Point Pond, about 15 miles west of Klamath Falls, Klamath County, Oreg., elevation about 4,300 feet ("*L. lemmoni*," Coopey, 1946, p. 339), 3 specimens clearly belonging to this species. Canada, with no particulars, 1♂, typical (U.S.N.M. No. 49121). Medicine Hat, Alberta, 2♂ (U.S.N.M. No. 54814).

Of material from Europe and Asia I have seen specimens from the following localities. Northern Siberia, Nikoulina, 1♂, Stockholm Museum No. 561; Igarskoj, 1♂, Stockholm Museum No. 1433; Worogoba, 1♂ and 1♀, Stockholm Museum No. 549; Jenissejsk, 2♀, Uppsala Museum; Mellraddinka, Kulundinsk Steppe, 2 specimens, (U.S.N.M. No. 82060.)

The species is further reported in America from Smithfield, Cache Valley, Utah (Packard, 1883). From the following places in Canada: near Winnipeg, Manitoba; Dufton, Saskatchewan (Johansen, 1921). Outside America, it is given (as *L. macrurus*) from Arkhangel (Lilljeborg, 1877), Government of Wolodga (Decksbach, 1924), Koslow, in Government of Tambow (Decksbach, 1924), Government of Rjasan (Smirnov, 1936), Northern Caucasus (Smirnov, 1932), all in the

TABLE 1.—*Morphological characters of specimens of* Lepidurus packardi, L. couesii, *and* L. bilobatus

Species and locality	Sex	Body-rings	Leg-bearing abdominal rings	Legless abdominal rings	Teeth, ventral half, last body-ring	Dorsal spines on supra-anal plate	Total length (mm.), less supra-anal plate and caudal filaments	Length (mm.), supra-anal plate	Length (mm.), caudal filaments	Length (mm.), fifth endite of first leg	Length (mm.), carapace	Width (mm.), carapace	Length: width relation, carapace	Length supra-anal plate in % length of carapace
L. packardi from Davis, Calif., U.S.N.M. No. 82030	♂	28	12	5	13	4	20	6	--------	4. 5	18. 5	2 x 9. 5	1. 03	32
	♀	27	11. 5	4. 5	17	14	19. 5	5	16. 5	6	18	2 x 9	1. 00	28
	♀	28	12	5	20	19	35	8. 5	>27	10. 5	30. 5	2 x 15	. 99	28
L. packardi from Lassen County, Calif., U.S.N.M. No. 9377	♂	28	11	6	17	10	24. 5	5. 5	>19	6. 5	17. 5	2 x 10	1. 14	31
	♂	27	10. 5	5. 5	17	9	22	5. 5	>20	6	17	2 x 10	1. 18	32
L. couesii from Montana (cotypes), U.S.N.M. No. 11605	♂	25	9. 5	4. 5	15	51	------	>6	25	7	20. 5	2 x 10. 5	1. 02	>29
	♂	------	------	4	19	43	------	8	--------	5	20	2 x 10	1. 00	40
	♀	27	11. 5	4. 5	18	22	23	4	--------	4. 5	22	2 x 12	1. 09	18
L. couesii from Montana (cotypes), Stockholm Museum	♂	26	10. 5	4. 5	16	64	24	7	--------	7	18	2 x 10	1. 11	39
	♂	26	10. 5	4. 5	19	35	20	8	--------	7. 5	19	2 x 10	1. 05	42
L. couesii from Idaho, 25 miles north of Ashton, U.S.N.M. No. 55800	♂	27	10. 5	5. 5	28	>100	21	6. 5	22. 5	4. 6	17. 5	2 x 10	1. 14	37
	♂	26	10. 5	4. 5	20	60	17	5	18. 5	5	15	2 x 8. 5	1. 13	33
	♀	26	11	4	18	29	15	2. 5	--------	3. 2	15	2 x 8	1. 07	17
	♀	26	11	4	20	68	18. 5	4. 5	18. 5	4. 2	18	2 x 9. 5	1. 06	25
L. couesii from Medicine Hat, Alberta, U.S.N.M. No. 54814	♂	26	10	5	18	37	13	5	11. 5	3. 5	12. 5	2 x 7	1. 12	40
	♂	26	10. 5	4. 5	18	>30	11	------	> 7	3	10	2 x 5. 5	1. 10	----
L. couesii from Max, N. Dak., U.S.N.M. No. 67699	♀	26	10	5	19	>75	------	7. 5	21. 5	4. 5	25. 5	2 x 13. 5	1. 06	29

L. couesii from Nikoulina, N. Siberia, Stockholm Museum No. 561	♂	27	11	5	23	25	18	5	21	7	18	2 x 10. 5	1. 17	28
L. couesii from Igarskoj, N. Siberia, Stockholm Museum No. 1433	♂	26+i	10. 5	4. 5+i	22	20	18. 5	4. 5	17	6	19. 5	2 x 10. 5	1. 08	23
L. couesii from Worogoba, N. Siberia, Stockholm Museum No. 549	♂ ♀	26 27	10 11	5 5	20 21	58 42	23 19. 5	8 5. 2	21 >15	8 5. 5	18 19	2 x 10 2 x 10	1. 11 1. 05	44 27
L. couesii from Jenissejsk, N. Siberia, Uppsala Museum	♀ ♀	26 27	10 10. 5	5 5. 5	18 22	51 21	20 19	6. 4 4	27 16	8 5. 5	21. 5 16	2 x 12 2 x 9. 5	1. 12 1. 19	30 25
L. bilobatus from Utah, U.S.N.M. No. 11606	♀	32	16. 5	4. 5	19	------	24	3. 5	------	-- 4. 5	15. 5	2 x 9	1. 16	23
L. bilobatus probably from Arizona, U.S.N.M. No. 82028	♀	32	16. 5	4. 5	28	------	38	7	------	--------	28	2 x 19	1. 36	25

European part of the U. S. S. R.; Jakutsk (Sars, 1897), several places in the territory of Akmolinsk (Sars, 1901, 1903), territory of Kokschetavsk (Sars, 1903), and Kasalinsk in Turkestan (Decksbach, 1924).

Remarks.—Outside America, there is a species with a similar telson and supra-anal plate, *L. macrurus* Lilljeborg. The general resemblance between this species and *L. couesii* was noted by Lilljeborg, who mentioned (1877, p. 14) one difference only, that the former has 6 to 8 rings exposed behind the carapace and the latter only 5. This character "is generally recognized to be somewhat unreliable" (Gurney, 1923, p. 502) because of the varying state of contraction of the specimens (p. 5), and I have seen American specimens of *L. couesii* with 7 exposed rings as well as specimens of *L. macrurus*, identified by Lilljeborg, with five exposed rings.

I have examined 25 Asiatic specimens identified as *L. macrurus* by Lilljeborg. They, as well as some specimens from a more southern locality, agree perfectly well with the American specimens of *L. couesii* as described, and ought to bear the same name, which is 2 years older than that given by Lilljeborg.

The relationship of this species to the European *L. apus*, to which it bears a certain resemblance, is in need of clarification, but I have not had enough material of the latter species to make a detailed comparison.

LEPIDURUS BILOBATUS Packard

Figure 13; Plate 2 (Figures 3, 4)

Lepidurus bilobatus Packard, 1883, p. 318.

Description.—A supplementary description of a female labeled "Type, Utah, coll. Henshaw" (U.S.N.M. No. 11606) is given here. Body-rings $11+16.5+4.5=32$. Legless rings with many (19) densely crowded spines on the ventral side, dorsally 7 spines. Supra-anal plate slightly bilobed, with 8 dorsal spines, 4 of which are smaller than the others, all of them placed on a slightly marked keel. Nuchal organ oval, placed between hind parts of eye-tubercles. About 62 pairs of legs. In other respects there is reasonable agreement with Packard's description. Further particulars are given in table 1 (p. 36).

Remarks.—The real status of this type seems to be a little uncertain, because Packard's type locality was not Utah, but Po Cañon, Vermillion River, Colo. However, the specimen most probably comes from Packard's collection, and I feel reasonably certain that it belongs to this species. The large number of abdominal rings agrees well with Packard's statements that "the abdomen is longer than usual" and "there are about sixteen segments beyond the posterior edge of the carapace." Another species with many abdominal rings is described later on in this paper (p. 39), but *L. bilobatus* is easily distinguished by the position of the nuchal organ, the typical arrangement of the spines on the posterior emargination of the carapace, and by the varying sizes of the spines on the supra-anal plate. In the two last mentioned respects, there is good agreement with Packard's description. "Seven more or less well-marked median spines" on the telson, according to Packard, stands in sufficiently good accordance with the condition in this specimen. Bilobation of the supra-anal plate occurs here, in agreement with Packard's description, but it is to be remembered that this character is not an important one.

Tentatively, I have placed here another specimen (U.S.N.M. No. 82028) which bears only the label "Probably Arizona."

In a case like this, when there is a little uncertainty about the status of the single existing type specimen, and the original description is not very good, it may be questionable whether we ought to discard the species or keep it on record. In my opinion, the description is good enough to enable us to identify the species with reasonable accuracy. However, it seems desirable to search for more material from the type locality or its vicinity.

LEPIDURUS LYNCHI, new species

FIGURES 14–18; 19, *c;* 20–27; PLATES 3, 4, AND 7 (FIGURE 3)

Type specimens.—Holotype (1 ♀), allotype (1 ♂), and paratypes (Uppsala Mus.); paratypes also in U.S.N.M. (No. 82101); ponds in the upper Grand Coulee, Grant County, Wash; collector J. E. Lynch. Additional paratypes (6♀♀, 2♂♂, 5 juniors) from Fish Lake Valley, Nev.; collector, La Rivers.

FEMALES (52 specimens): Holotype 11+16.5+4.5=32 body-rings; paratypes 11+(15–18)+(3+i–5.5)=30+i–34 body-rings. Surface of all body-rings smooth, spines on dorsal and lateral quarters of caudal border of legless rings large, smaller on ventral quarter. On penultimate ring 9 large, 8 small spines; in paratypes 6–14 and 4–9, respectively, the boundary between large and small spines not always sharp, because they may diminish in size gradually. Telson (disregarding supra-anal plate) long, its length almost as great as its width, smooth except for small spines around dorsal sense organs and around bases of caudal filaments. Supra-anal plate 4 mm. in length (24 percent of carapace); in paratypes 0.6–8 mm. (7–30 percent of length of carapace, highest percentage being in large specimens). This plate irregularly tongue-shaped, with coarse, small spines on its margin, and 4 rather large spines dorsally in midline; in paratypes broadly triangular, tongue shaped or spatulate, often more or less bilobed, often irregular, with 2–7 dorsal spines. Caudal filaments 24 mm.; in paratypes 11–39 mm. 18 body-rings exposed beyond carapace; in paratypes 12–19. Color of preserved specimens greenish brown. Total length disregarding supra-anal plate and caudal filaments, 26 mm.; paratypes 12–45.5 mm. (preserved specimens!).

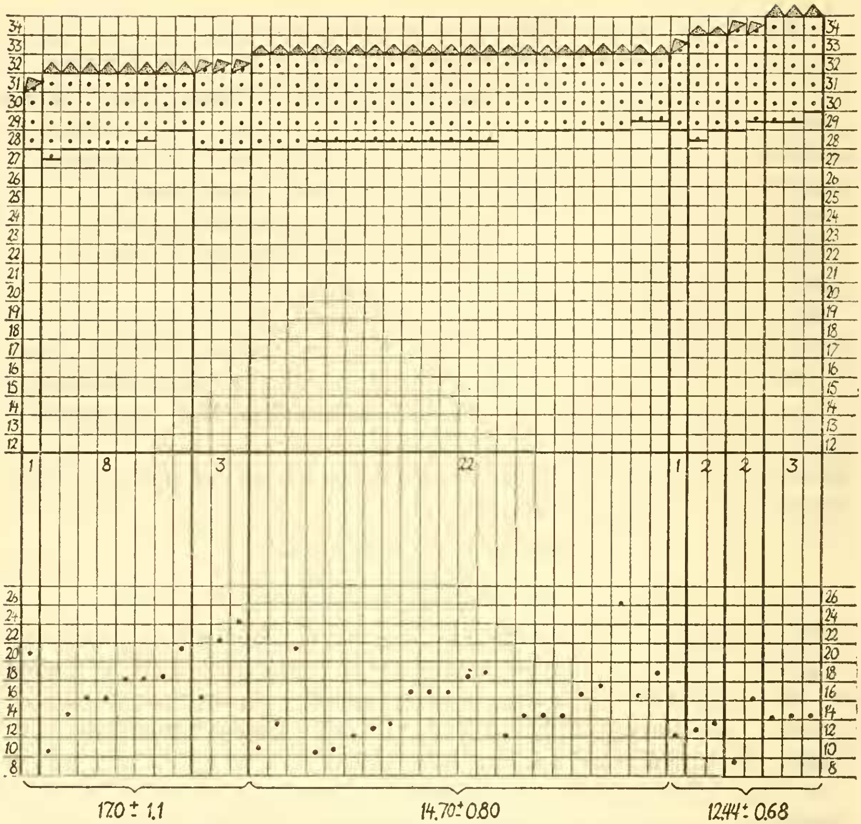

FIGURE 14.—Diagram indicating the number of body-rings in the abdomen and the length of the carapace in 42 female paratypes of *Lepidurus lynchi*, new species (males present in the sample not considered here). Each shaded triangle at the top of the diagram represents the telson of a specimen, below which are indicated the legless abdominal rings (dotted) and the leg-bearing rings. Incomplete rings at the anterior boundary of the telson are denoted by the oblique position of the triangle. Body-ring numbers are shown in the marginal columns at the left and right of this portion of the diagram. The carapace length of each specimen in mm. is indicated in the lower part of the figure, according to the scale in the left and right marginal columns. Correlations of various kinds are reserved for a later statistical report on more comprehensive material.

Carapace length 17.5 mm.; width 2 x 11.5 mm., width: length relation 1.22; in paratypes length 8.5–26 mm., width 2 x 5–2 x 15 mm., width: length relation 1.14–1.30. Caudal half of lateral margin serrated by numerous, minute, pointed spines. Dorsal carina slightly marked, with 19 short spines evenly scattered along whole carina; in paratypes carina often inconspicuous or wanting, with 0–20 spines. Posterior emargination rather deep, 5 mm., with 12 short spines on one side, 13 on the other, not quite similar in size and somewhat irregularly placed; in paratypes 7–17 spines on each side. Supra-antennal crest quite smooth.

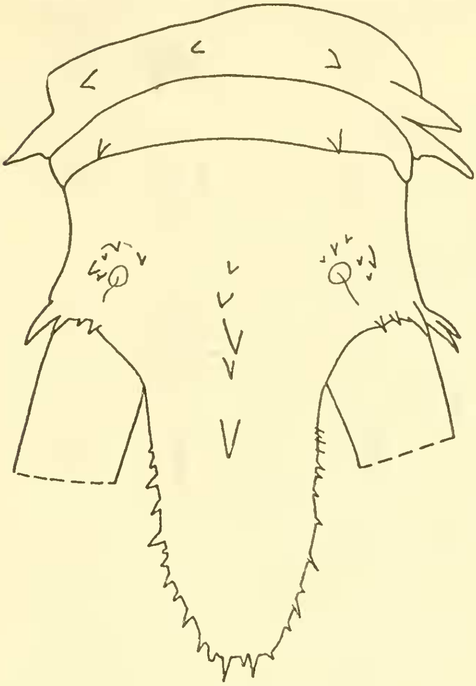

FIGURE 15.—Dorsal view of telson and last two body-rings of a female of *Lepidurus lynchi*, new species, × 18.

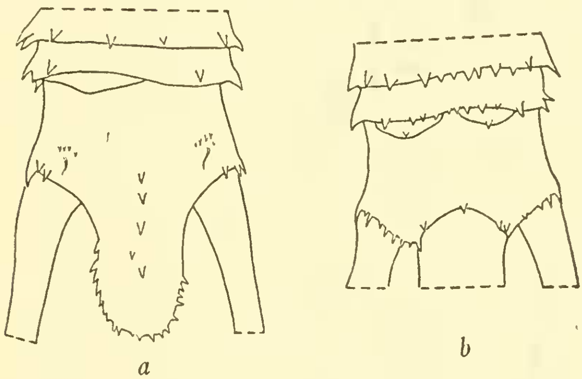

FIGURE 16.—Three pieces of an incomplete ring at the anterior margin of the telson in a female of *Lepidurus lynchi*, new species, × 11: *a*, Dorsal view; *b*, ventral view.

Eyes unusually small. Nuchal organ round, elevated to about same height as the small eye-tubercles, and placed clearly behind them; in paratypes more or less rounded form, rather varying height but always similar in position.

Antennae, mandibulae, and maxillae as usual in the genus.

Pairs of legs 61; in paratypes 60–71. Endites 2, 3, 4, 5 on first leg 1, 5, 3.4 and 8 mm., long, respectively; endopodite very short,

TABLE 2.—*Arrangement of legs in five females of* Lepidurus lynchi, *new species, and three males of* Apus longicaudatus *LeConte; each lot from a single locality.* (See p. 7.)

Item	*Lepidurus lynchi* (5 females)					*Apus longicaudatus* (3 males)		
Length carapace (mm.)	12	12	13	18	25. 5	14	14. 5	19
Number leg-bearing abdominal body-rings	16. 5	16. 5	17	16. 5	16	17	19	17
Number pairs legs	63	64	66	66	68	59	57	58
Leg-bearing abdominal body-ring on which 50th pair of legs is placed.	Beginning of 16th	Near end of 15th	Middle of 15th	End of 15th	End of 14th	Beginning of 17th	End of 18th	Beginning of 17th

TABLE 3.—*Numbers of legs and body-rings in the species of* Lepidurus *and* Apus. (See p. 17.)

Species	Total pairs of legs	Leg-bearing abdominal body-rings	Legless abdominal body-rings	Total body-rings
Lepidurus apus, arcticus, couesii, kirki, packardi, viridis, probably *patagonicus*	35–46	9.5–13	3.5–8	25–29
Lepidurus bilobatus, lynchi, lynchi var. *echinatus*	60–71	14.5–18	3–6	30–34
Apus australiensis, cancriformis, granarius, longicaudatus, namaquensis, numidicus, sudanicus (*A. cancriformis* may form a separate group, cf. p. 52).	50–66	12.5–21	4. 5+i–17	30–44

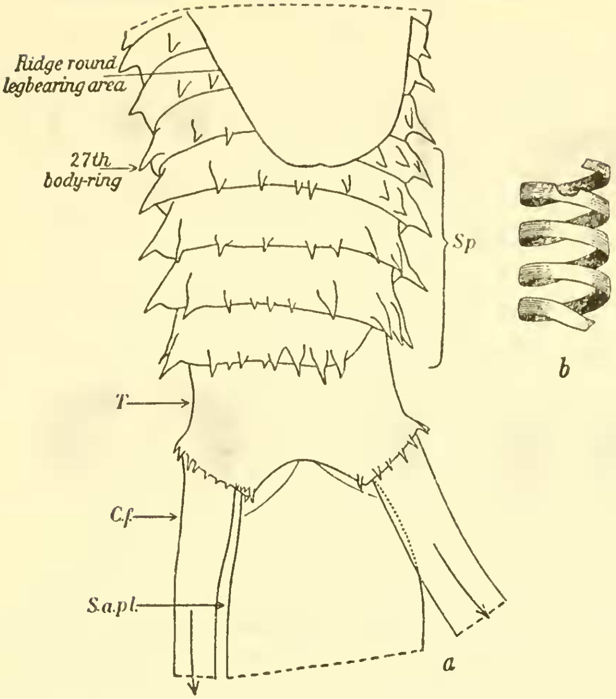

Figure 17.—*a*, Oblique ventral view of part of the abdomen and telson of the largest female; of *Lepidurus lynchi*, new species, showing a right-handed spiral of a little more than four rounds beginning in the leg-bearing part of the body and forming the entire legless part of it, × 8.5. The telson is shown in ventral view because of a slight natural torsion of the telson. Legs omitted, as well as spines on caudal filaments. Only basal parts of supra-anal plate and caudal filaments shown. (*C.f.*, caudal filaments; *S.A.pl.*, supra-anal plate; *Sp*, spiral; *T*, telson.) *b*, Schematic drawing of the spiral.

Figure 18.—Dorsal view of posterior emargination of the carapace of a female paratype of *Lepidurus lynchi*, new species (Uppsala Museum), × 7.

fringed with setae on its caudal margin; in paratypes (fig. 21) varying lengths, but fifth endite always at least double the length of fourth and reaches, when stretched backward, usually nearly to the posterior angle of carapace. On second leg endites 3, 4, and 5 rather similar in length, endopodite long, 2.2 mm., pointed, of about same length as fifth endite, fringed with setae on its caudal margin. Eleventh leg with a small epipodite, fringed with setae, and trace of a pre-

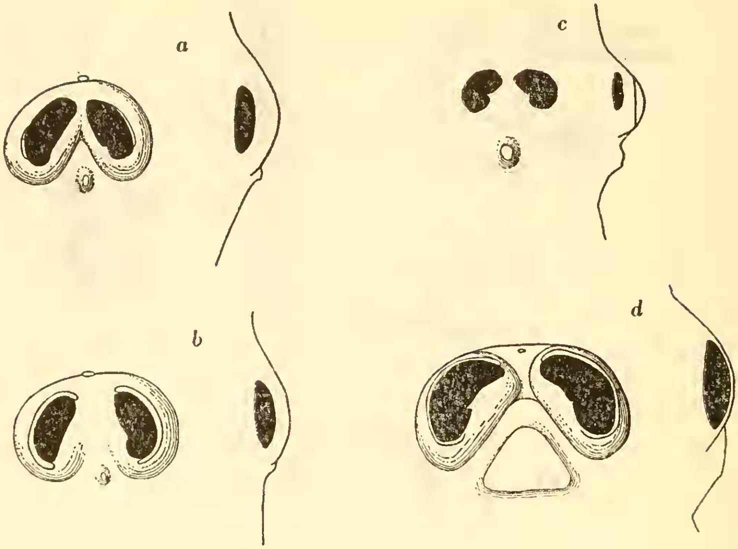

Figure 19.—Eyes and nuchal organ: *a*, Female holotype of *Lepidurus packardi* Simon (Paris Mus.), ×12; *b*, male paratype of *Lepidurus couesii* Packard from Montana (Stockholm Mus.), ×12; *c*, female paratype of *Lepidurus lynchi*, new species (Uppsala Mus.), ×8; *d*, male of *Apus longicaudatus* from Wyoming (U.S.N.M. No. 58766), × 8.

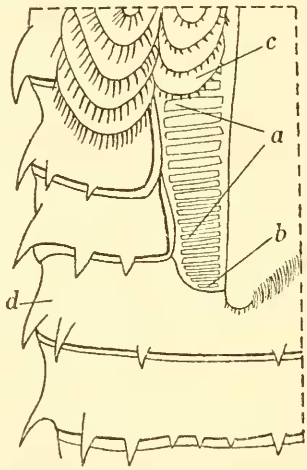

Figure 20.—Ventral view of a portion of the right side of a female of *Lepidurus lynchi*, new species, from which the last 25 legs have been removed, × 21. The specimen has 11+17.5+3.5=32 body-rings and 64 pairs of legs. *a*, Bases of legs; *b*, base of last (sixty-fourth) leg; *c*, endopodite of thirty-ninth leg; *d*, twenty-ninth body-ring.

epipodite in the form of an elevation with a few setae. Last leg very small.

Males (55 specimens): Allotype 11+14.5+4.5+i=30+i body-rings; paratypes 11+(14.5–17)+(3.5–5.5)=30–33+i body-rings. Surface of body-rings smooth, spines on caudal border of legless rings about as numerous as in female. Telson, except supra-anal plate, as in female. Supra-anal plate 6.5 mm. in length, 35 percent of length of carapace; in paratypes 0.7–5 mm., 18–32 percent of length of carapace. This plate irregularly bilobed, with 2 rather large spines dorsally in midline; in paratypes form varying as in female, with 2–6 spines. Caudal filaments 23 mm.; in paratypes 14–25.5 mm. Body-rings exposed behind carapace 15+i; in paratypes 10–19. Color as in female.

Total length without supra-anal plate and without caudal filaments 29.5 mm.; paratypes 12–24 mm.

Carapace length 18.5 mm., width 2 x 11 mm., width: length relation 1.19; in paratypes length 11.5–16.5, width 2 x 7–2 x 10 mm., width: length relation 1.08–1.33. Anterior part broader than in females. Spines on lateral margin of carapace as in females. Carina missing; one short spine in midline; in paratypes sometimes trace of an inconspicuous carina at the places where there are spines, these ranging

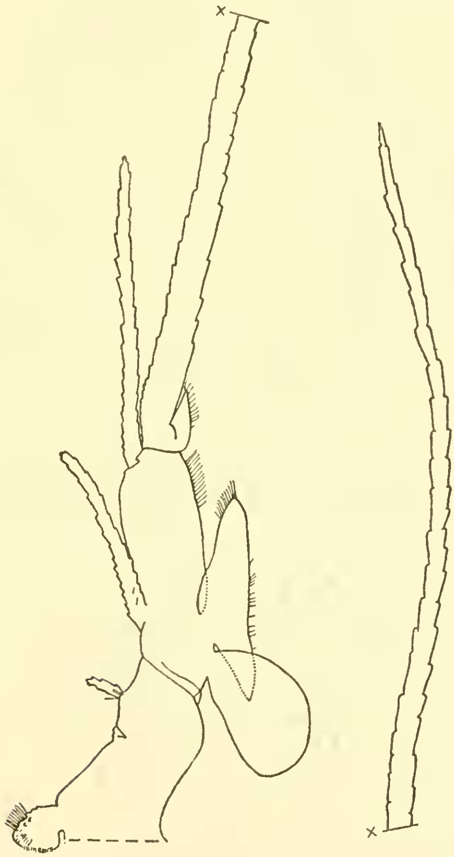

FIGURE 21.—First leg of a female paratype of *Lepidurus lynchi*, new species (Uppsala Mus.), × 6.

from 0–28 in number. Posterior emargination rather deep, 5 mm. in depth, with 13 rather conspicuous spines on one side, 14 on the other, a little irregularly placed and not quite similar in size; in paratypes rather deep, 7–16 spines on each side.

Eyes, nuchal organ, and supra-antennal crest as in female.

Antennae, mandibulae, and maxillae as in female.

Pairs of legs 60; in paratypes 60–67 (only 5 specimens counted). Length of endites 2, 3, 4, and 5 on first leg 0.8, 3.4, 4 and 10.2 mm., respectively; endopodite very short, fringed with setae on its caudal margin; in paratypes varying lengths, but fifth endite always more than double the length of fourth endite, reaching, when stretched backward, more than halfway to end of carapace. On second leg

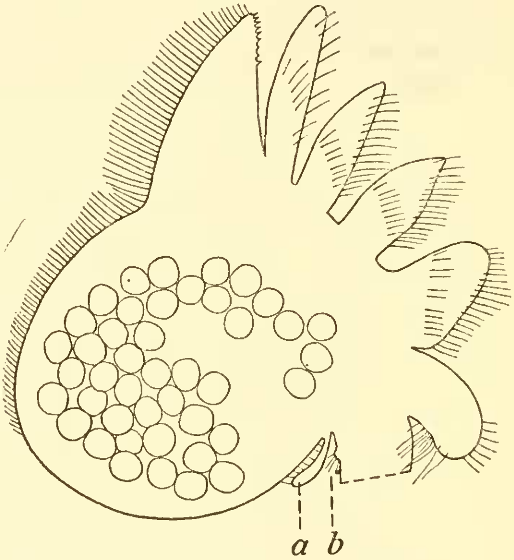

FIGURE 22. Eleventh leg of a female paratype of *Lepidurus lynchi*, new species (Uppsala (Mus.), × 12: *a*, Epipodite; *b*, pre-epidodite.

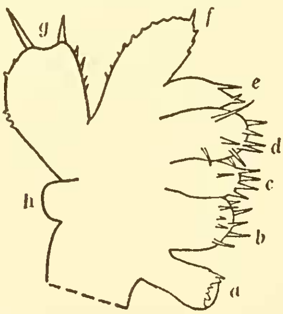

FIGURE 23.—Last (seventy-first) leg of a female paratype of *Lepidurus lynchi*, new species (Uppsala Mus.), × 200: *a-e*, First to fifth endite; *f*, endopodite; *g*, exopodite; *h*, epipodite.

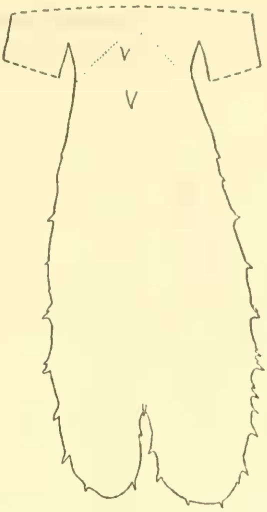

FIGURE 24.—Dorsal view of supra-anal plate of a male paratype of *Lepidurus lynchi*, new species (Uppsala Mus.), × 10.5.

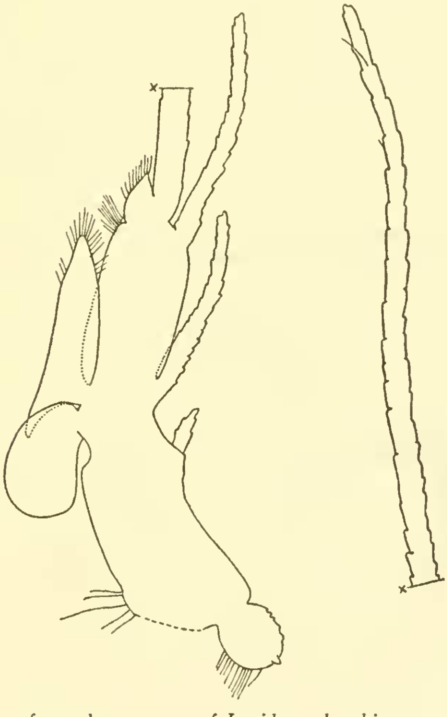

FIGURE 25.—First leg of a male paratype of *Lepidurus lynchi*, new species (Uppsala Mus.), × 7.

endites 3 and 4 of same length, 2.1 mm., endite 5, 4.2 mm., endopodite long and narrow, 2.2 mm., fringed with setae on its caudal margin;

in paratypes varying lengths, fifth endite sometimes not much longer than endopodite. Eleventh leg with trace of a pre-epipodite as in female.

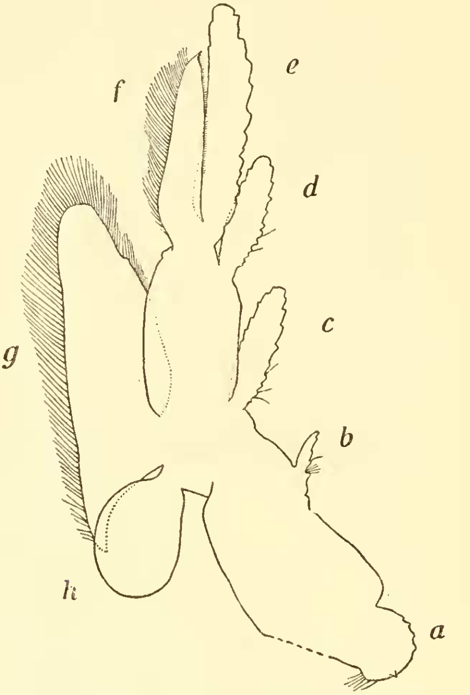

FIGURE 26.—Second leg of male paratype of *Lepidurus lynchi*, new species (Uppsala Mus.), × 7: *a-e*, First to fifth endite; *f*, endopodite; *g*, exopodite; *h*, epipodite.

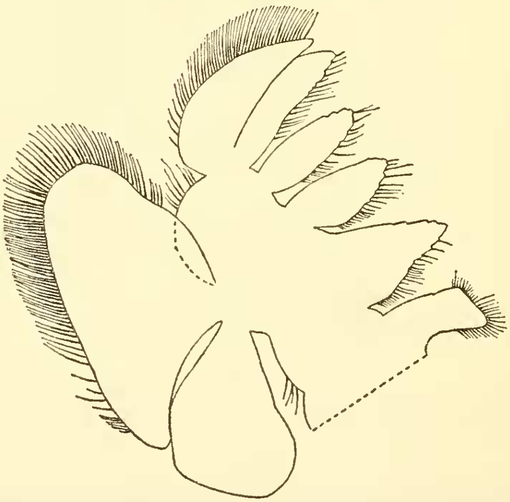

FIGURE 27.—Eleventh leg of a male paratype of *Lepidurus lynchi*, new species (Uppsala Mus.), × 13.

Remarks.—This new species is especially interesting, because it belongs (see table 3) with *L. bilobatus* in the group with many abdominal rings. The variation of the species, as limited above, may perhaps seem to be rather great. It includes forms with a very spiny carapace together with forms where the carapace is quite smooth; but intermediate forms occur in great numbers, and we find a similar variation in several species of the genus *Apus* (Barnard, 1929). Furthermore, the form of the supra-anal plate is highly variable; but, as I have shown previously (p. 26), this is true of many species. The great range of variation must be seen in connection with the fact that the species is described from such a great number of specimens from the same district.

The species is easily distinguished from *L. bilobatus* by the size and place of the nuchal organ and the eyes, characters to which I must ascribe great taxonomic importance. Its relation to the following form, however, I cannot regard as quite clear.

LEPIDURUS LYNCHI ECHINATUS, new variety

FIGURE 28; PLATES 5 (FIGURE 1), AND 7 (FIGURE 4)

Type specimens.—Holotype ♀ (U.S.N.M. No. 82068), allotype ♂ (U.S.N.M. No. 82069), paratypes 6 ♂ and 4 ♀ (U.S.N.M. No. 82070 and Uppsala Mus.). North end of Goose Lake, about 15 miles southwest of Lakeview, Lake County, Oreg.; altitude 4,700 feet; in water 2 feet deep, muddy; June 14, 1940; collector, J. E. Lynch.

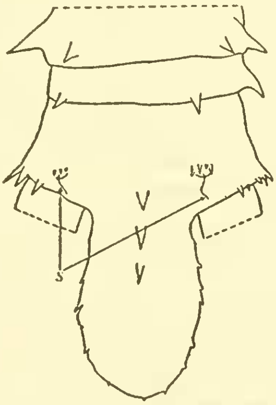

FIGURE 28.—Dorsal view of telson and last two body-rings of a female of *Lepidurus lynchi echinatus*, new variety, × 9. (*S*, dorsal sensory setae.)

Body-rings 11+(16–17.5)+(3.5–4.5)=31–33. Telson rather long. Always many large spines on carina of carapace. In females, 2–5 dorsal spines on supra-anal plate, in males, 3. Legs 67–68 in number (only two specimens). Total length, disregarding supra-anal plate and caudal filaments: Female 32–41 mm., male 22–30 mm. Length of carapace: Female 21–28 mm., male 17.5–21 mm. Width: length relation of carapace 1.21–1.29.

Very similar to the typical form. All characters lie within the range of variation mentioned for this form, except for some details of the carapace. On the middle and caudal part of its lateral margin there are numerous stout spines considerably larger than those in the principal form, though not so large as the spines at the posterior emargination. All the first-mentioned spines are directed straight outward. This is a very conspicuous feature and the explanation of the name *echinatus*. Furthermore, the carapace is more rounded and a little larger in relation to the body than in the typical form, and its posterior emargination is less deep, leaving a smaller number (7–10) of rings exposed behind the carapace.

Remarks.—It is regrettable that there are not more than 12 specimens of this variety, because this small lot cannot be expected to show much of the variation. As a provisional measure I have given it the rank of a variety within *L. lynchi*, because it shows a great similarity to this species in such important respects as the number of abdominal rings, the characteristic appearance of the eyes and the nuchal organ, and the array of spines on the lateral margins of the carapace. At the same time, there are clear differences between the two forms in the shape of the carapace.

There is a certain similarity between this variety and *L. lemmoni* Holmes, especially in the array of lateral spines on the carapace and, perhaps, also in the position of the nuchal organ.

But, as I will discuss in more detail later (p. 51), the similarities are more or less uncertain, and I consider *L. lemmoni* as an insufficiently known species. There are dissimilarities, in any event, among which the different shape of the posterior emargination of the carapace is the first to attract attention. I consider it better in this case to establish a new variety than to venture a highly dubious identification with an insufficiently described species.

LEPIDURUS LEMMONI Holmes

Lepidurus lemmoni Holmes, 1894, p. 585 (not Coopey, 1946, p. 338).

Description.—The principal points of the description of this insufficiently known species follow: About 4 body-rings exposed behind carapace, 4 or less legless body-rings (the author says 5 instead of 4, but in all probability he counts the telson as a ring). Number of spines on last body-ring never far from 12. Supra-anal plate rather long and may be rounded, truncated (obliquely so in some specimens), or, in some cases, bilobed, with 2–3 spines in midline, but no median carina except where the spines are situated. Carapace oval, carina with 10–15 teeth, posterior emargination with 5–7 teeth, sides with numerous small teeth. Nuchal organ round, small, considerably elevated, and located considerably behind the posterior margin of eyes. Length, 28 mm.

Type locality.—Honey Lake, Calif.

Types.—The type specimens (4 ♀, 1 ♂) are said to have been lost in the San Francisco fire.

Remarks.—Holmes' description is very good for its time, but naturally it does not mention the number of abdominal leg-bearing rings or the total number of rings. In these respects, there are two well demarcated groups within the genus, and these totals seem to be essential for a proper identification. Perhaps both were low, because he reports only 4 rings exposed behind the carapace; but we cannot be certain of this. Equivalent totals in *L. lynchi* var. *echinatus* are high even though as few as 7 rings are exposed. Only 12 specimens are known of the latter form, and only 5 of *L. lemmoni*. So few specimens cannot be expected to show a full range of variation; thus, it is possible that *L. lemmoni* may fall in within the upper limits of variation in this respect. And we must not forget that, in general, the number of exposed rings is shown to be an unreliable character, so its value as an indicator of the number of rings is very uncertain.

Other characters do not give clear indications, either. The nuchal organ is "located considerably behind the posterior margins of the eyes." Perhaps we have a condition here similar to that in *L. lynchi* and *L. lynchi* var. *echinatus*, but a precise comparison is impossible because Holmes does not mention the place of the organ in relation to the eye-tubercles, only to the eyes.

The very long caudal filaments present a character of doubtful significance. In each large lot of *Lepidurus* there is considerable variation in the length of these appendages.

The lateral spines on the carapace look quite conspicuous on Holmes' figure. Similar spines, or larger still, are found in *L. lynchi* var. *echinatus*, whereas in all other notostracans I have seen the corresponding structures are minute and inconspicuous. But *echinatus* differs clearly from *L. lemmoni* by its very shallow posterior emargination of the carapace as well as by the structure of its legs, and so an identification with this form seems highly improbable.

To sum up, the characters given for *L. lemmoni* cannot be regarded as sufficient for a proper identification. In my opinion, we had better not keep the species on record.

It can be abandoned without much trouble, because, as far as I can see, it has been recorded only once since its establishment, and in this case there is undoubtedly an error of identification. Coopey (1946) refers some specimens from Oregon to this species, though with the express reservation that they are only provisionally identified. Most kindly, he has given me the opportunity of examining 3 specimens from Rocky Point Pond, Klamath County. I find them to belong to *L. couesii*. The telson (without supra-anal plate) is short and broad, and on the conspicuous keel of the supra-anal plate there is a large number of spines of varying sizes (2–3 spines in *L. lemmoni*). Even the place of the nuchal organ is as in *L. couesii*. All characters considered, the specimens are quite typical representatives of this species.

Genus APUS Schaeffer

Apus Schaeffer, 1756, p. 131.—Gurney, 1923, p. 497.—Barnard, 1929, p. 229.[1]

The principal characters of the genus are, in my opinion, the absence of a supra-anal plate on the telson (p. 26), the relatively large number of body-rings, 30–44 as against 25–34 in *Lepidurus* (p. 42), and the reduction of the second maxillae in full-grown specimens (p. 28).

Even within these limits, however, the genus presents a unit that is not quite homogenous or well distinguished from the genus *Lepidurus*, because one species, *A. cancriformis*, is in several respects suggestive of the latter genus.

Absence of a supra-anal plate seems to be characteristic of all species except *A. cancriformis*, where we may find something rather similar to such a plate (fig. 8). It is very short, but we can only assume that it is essentially the same structure as the plate in *Lepidurus*, so that *A. cancriformis* may be regarded as an intermediate stage, in this respect, between *Lepidurus* and the remaining species of *Apus*.

In the reduction of the second maxillae, the same species forms an exception. I have found it to have, in full-grown specimens, just as well developed maxillae as in any species of *Lepidurus*.

It has very few body-rings as compared with almost all the other species of the genus that I have examined. There are a minimum of 30, and, generally, a maximum of 34. In only one sample of *A. cancriformis* have I found more, 35 in a female and 35 or 37 in the males (U.S.N.M. No. 58211, from Nanking, China). I have observed a similarly small number of rings in *A. sudanicus* from South Africa, identified by Barnard (U.S.N.M. No. 75749). The male in this sample has 32, the two females 33 and 33+i body-rings. All the other species of *Apus* have a larger number of body-rings. *A. longicaudatus* comes nearest with 34+i–44 rings (see table 4); however, I am fully aware that in many forms we know too little of the number to be able to make definite groupings of the species according to this character. Still, it may be considered significant that *A. cancriformis*, which comes close to Lepidurus in the structure of the telson and the second maxillae, also has a similar total number of body-rings. This is a further indication that the species is a sort of connecting link between the two genera.

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[1] I fully agree with Gurney and Barnard that the name of *Triops* Schrank, 1803, pp. 180, 251 (sometimes spelled *Triopes* or *Thriops*), ought to be rejected.

In its general appearance, also, this species is suggestive of the genus *Lepidurus*. The body, because of its small number of rings, may be almost completely covered by the carapace, which sometimes leaves only part of the telson exposed. Such proportions are unusual in the species of *Apus*, and it is interesting to notice that they occur, not in the species of *Lepidurus* that have a similar number of rings (*L. bilobatus*, *L. lynchi*), but in those that have the fewest rings.

The number of abdominal leg-bearing rings, a figure that proved helpful as a means of distinguishing groups within the genus *Lepidurus* (p. 31), gives no clear character in *Apus*. In the whole genus, it ranges from 12.5 to 20, figures that are generally higher than in *Lepidurus*. Im *A. cancriformis*, the range is usually 16 to 18, though I have occasionally observed either fewer or more of such rings (the fewest was noticed, not in this species, but in *A. sudanicus*, as noted above, where a male has 12.5 and two females 13.5 and 14 such rings).

The number of pairs of legs in various species is too little known to enable us to draw any conclusions about its taxonomic value.

On the whole, we must admit that much work remains to be done before we will be able to make a reasonably good arrangement of the species of *Apus*.

Distribution in America: Montana, Oregon, Wyoming, California, Nevada, Utah, Colorado, Nebraska, Arizona, New Mexico, Kansas, Oklahoma, Texas; Galápagos Islands; Hawaiian Islands; Mexico; Haiti; St. Vincent Island; Argentina.

APUS LONGICAUDATUS LeConte

Figures 3–6, 19, *d*, 29–31: Plates 5 (Figures 2, 3), 6, and 7 (Figures 1, 2)

Apus longicaudatus LeConte, 1846, p. 274.—Packard, 1883, p. 324.—Mackin, 1939, p. 46.
Apus aequalis Packard, 1871, p. 3; 1883, p. 320.—Pearse, 1912, p. 192; 1913, p. 2.
Apus newberryi Packard, 1871, p. 2; 1883, p. 321.
Apus lucasanus Packard, 1871, p. 2; 1883, p. 322.
Apus oryzaphagus Rosenberg, 1947, p. 70.
Apus biggsi Rosenberg, 1947, p. 72.

As far as I can see, the various species of *Apus* described from the North American continent must be united into one species, *A. longicaudatus*. A study of reasonably extensive material shows that the three species of Packard, enumerated above, cannot be properly demarcated from each other and from *A. longicaudatus*, and the same applies to Rosenberg's species.

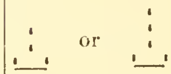
Packard's material was probably too limited to enable him to detect the unbroken series of variation in most of the characters used by him. It was not so much that he had material from so few localities—4 species from 13 localities—as that only a few specimens were available from each locality. One of his species, *A. newberryi*, was based upon three females from two localities.

TABLE 4.—*Total number of body-rings observed in various species of* Apus

Species	Number of specimens	Males																										
		31	+i	32	+i	33	+i	34	+i	35	+i	36	+i	37	+i	38	+i	39	+i	40	+i	41	+i	42	+i	43	+i	44
cancriformis, South Africa, U.S.N.M. No. 75747	2	x																										
cancriformis, England, U.S.N.M. No. 5857																												
sudanicus, South Africa, U.S.N.M. No. 75749	1			x																								
cancriformis, Eritrea, Uppsala Mus.																												
cancriformis, Sweden, Uppsala Mus.																												
longicaudatus, many localities (table 8)	64															x	x	x		x	x	x	x	x	x	x	x	x
cancriformis, Nanking, China, U.S.N.M. No. 58211	2									x				x														
australiensis, Cowcowing, Western Australia, Uppsala Mus.	1																	x										
numidicus, South Africa, Stockholm Mus.	30																		1	6	1	12	5	3	2			
granarius, Kansu, China, Stockholm Mus.	13																		1		3	6	3					
australiensis, Lake Gidgee, Western Australia, Uppsala Mus.	7																	1				5		1				
granarius, Shansi, China, Stockholm Mus.	23																					5	9	8		1		
namaquensis, South Africa, U.S.N.M. No. 75748	1																										x	

Species	Number of specimens	Females																										
		30	+i	31	+i	32	+i	33	+i	34	+i	35	+i	36	+i	37	+i	38	+i	39	+i	40	+i	41	+i	42	+i	43
cancriformis, South Africa, U.S.N.M. No. 75747	3	x		x		x																						
cancriformis, England, U.S.N.M. No. 5857	2							x																				
sudanicus, South Africa, U.S.N.M. No. 75749	2							x	x																			
cancriformis, Eritrea, Uppsala Mus	10							x		x																		
cancriformis, Sweden, Uppsala Mus	32							28	2	1	1																	
longicaudatus, many localities (table 8)	135										x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x
cancriformis, Nanking, China, U.S.N.M. No. 58211	1											x																
australiensis, Cowcowing, Western Australia, Uppsala Mus	2																	x										
numidicus, South Africa, Stockholm Mus	30																	2	1	7	2	8	1	8		1		
granarius, Kansu, China, Stockholm Mus	10																	1		2	4	3						
australiensis, Lake Gidgee, Western Australia, Uppsala Mus	8																			3	1		3	1				
granarius, Shansi, China, Stockholm Mus	29																			2	2	14	5	4		2		
namaquensis, South Africa, U.S.N.M. No. 75748	2																						x					

TABLE 5.—*Chief characters of the species of* Apus *recognized by Packard*

Species	Carapace	Exposed rings	Legless rings	Telson	Pattern of dorsal central spines on telson
A. aequalis	As long as abdominal portion behind it.	♂22 ♀24	♂10 ♀8	Short	
A. newberryi	Shorter than in *aequalis*	♀28	♀10	Longer than in *aequalis*	
A. lucasanus	Shorter than in *newberryi*	♂32 ♀28	♂12 ♀10	Longer than in *longicaudatus*	
A. longicaudatus	Shortest of all American species	♂31 ♀27	♂13 ♀9	Very short	

I suspect that many carcinologists have had difficulties trying to identify species of *Apus* with the aid of Packard's descriptions. Pearse (1912) gives a good example. He had an unusually large number of specimens from one locality and found a remarkable variation in the number of dorsal spines on the telson, which Packard uses as one of the main characters: "The armature of the telson is somewhat variable; on the dorsal side there is commonly one median spine, but there are often two; there are usually two lateral spines at the proximal edge of the telson, but there are frequently more" (Pearse, 1912). Here is a mixture of characters from several species. *A. lucasanus* and *A. longicaudatus* are described with one median spine, *A. aequalis* with two, as is one of the specimens of *A. newberryi* mentioned by Packard. "Lateral spines at the proximal edge of the telson," probably means the spines around the dorsal sensory setae, of which one on each side is described as large in *A. lucasanus*. Thus most of Pearse's specimens ought to have agreed with *A. lucasanus*, but others not. Further, Pearse found the length of the carapace to be "about equal to the portion of the body exposed behind," as in *A. aequalis* according to Packard; it was obviously on these grounds that he identified his specimens with this species and dismissed the similarities with other species (especially *A. lucasanus*), which were observed on the telson of most specimens.

Mackin (1939) says that Packard's three species are synonyms of LeConte's species; his studies on material from Oklahoma and neighboring States showed that the characters used by Packard are of little value in taxonomics. However, he regards his conclusion as only tentative.

Packard's descriptions cover a lot of characters, but many of them are considered in only one species, so that comparisons in some respects are impossible. Those presented in table 5 are especially stressed by him. (In this table I have, in all cases, given one less ring than Packard, because he obviously counts the telson as a body ring, while I do not.)

The length of carapace in relation to length of body, and the number of body-rings exposed behind the carapace, vary according to the contraction of the rings, a condition itself highly variable. These characters are, of course, also influenced by the number of body rings, though in a rather erratic way on account of the variable contraction of the rings. These characters of Packard's are not simple characters, and generally they are more or less unreliable.

As for the number of legless rings, the examples in table 6 show how greatly this often varies in specimens from the same locality. The sample from Wyoming (columns a, c) is significant. It contains many more specimens than the others, and it covers the numbers given by Packard as characteristic of three species, *A. newberryi*

(10 in females), *A. lucasanus* (10 in females), and *A. longicaudatus* (9 in females, 13 in males). More than that, it presents an unbroken series beginning with a number of legless rings not much greater than that given for *A. aequalis* and ending with a number (15+i) considerably higher than those observed by Packard. No correlation with other characters has been found.

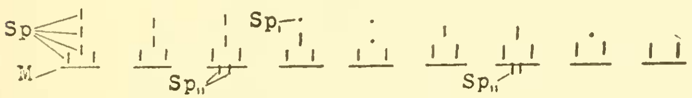
TABLE 6.—*Variation in the number of legless rings in populations of* Apus

Number of legless rings	Females		Males		
	U.S.N.M. No. 58766 (Wyoming) (a)	U.S.N.M. No. 61750 (Texas) (b)	U.S.N.M. No. 58766 (Wyoming) (c)	U.S.N.M. No. 61750 (Texas) (d)	Stockholm Mus. (Kansas) (e)
9+i	} 2				
9.5	}				
9.5+i	1				
10	6	5			
10+i	8	3			
10.5	7	2			1
10.5+i	7				
11	23	1			2
11+i	21				1
11.5	8				1
11.5+i	2				
12	8				
12+i	3			1	
12.5	1		1		
12.5+i				1	
13	1		4	4	
13+i			3	4	
13.5			1	3	
13.5+i			2	2	
14			8	3	
14+i			7		
14.5			2		
14.5+i					
15			4		
15+i			1		
Total specimens	98	11	33	18	5

The other lots in this table are too small to enable us to make conclusions of a similar degree of probability, though it is noteworthy that they show a small average number of legless rings. The lot from Kansas (column e), however, is interesting for the reason that these specimens were sent from Packard and labeled by him *A. lucasanus*. Thus we may regard them as paratypes of this species. But they do not agree with his description, which claims 10 legless rings in the female, 12 in the male. Here we find only 9 such rings in the female (not shown in table 6), 10.5 to 11.5 in the males, to which must be added a male with spiral growth where there are 8 ordinary rings and 2 spirals of 2 rounds each in the legless part of the abdomen. This lack of agreement between the paratypes and the description is significant, and it will be stressed when we find that they do not agree with the description in another respect, either.

I have seen many small lots of *Apus* from North America, in which the number of legless rings varied considerably. The material gives the impression that different populations might be characterized by different numbers, but this is by no means statistically certain, and I am convinced that this problem can be solved only by studying large lots. Also, we must not forget that the number of legless rings is quite a dubious character: it is the result of the interaction of the number of leg-bearing rings and the total number of rings.

Size and form of the telson are worth attention because this has proved a reasonably good character in *Lepidurus*. As did Packard, I have found some variation in this structure. However, the various forms present a reasonably continuous series, and I have not been able to discover any correlation with other characters. As the specimens in one lot are usually similar to each other as far as the telson is concerned, perhaps it ought to be determined whether the differences can be of some use in distinguishing lower taxonomical units.



		a	b	c	d	e	f	g	h	i	Total
1.	♂		5				34	1			40 } 154
	♀	1	12		1	1	92	1	1	5	114
2.	♂		2				16	1		1	20 } 37
	♀		3				14				17
3.	♂		1	1							2 } 2
	♀										–
4.	♂	1	1				3				5 } 6
	♀						1				1

Figure 29.—Patterns (a to i) of dorsal central spines on the telson in representative specimens of *Apus longicaudatus* LeConte from: (1) Near Aurora, Wyo. (U.S.N.M. No. 58766); (2) Moores Lake, Lubbock, Tex. (U.S.N.M. No. 61750); (3) Galápagos Islands (U.S.N.M. No. 84240); and (4) Kansas (Stockholm Mus., types of *A. lucasanus* Packard). M, dorsal hind margin of telson; Sp, well-developed spine; Sp_{I}, rudimentary spine; Sp_{II}, short spine.

Finally, in considering the pattern of the central dorsal spines on the telson, we must remember that Pearse found a considerable variation here, and that Rosenberg (1947) found the pattern variable in his material. My studies have shown that the variation presents a regular series with many intermediate patterns between the most common ones, so that in a sample with many specimens almost all patterns may be represented.

We see from figure 29 that some patterns are more common than others. These patterns were given the value of specific characters by Packard (1883); he assigned patterns a and b to *Apus newberryi*, pattern b to *A. aequalis*, pattern c to *A. longicaudatus*, and pattern f to *A. lucasanus*. Even in his small collection, however, significant variations must have been known to him. He gives two different patterns for *A. newberryi*, while the paratypes of *A. lucasanus* that

TABLE 7.—*Characteristics of type specimens of* Apus aequalis, A. newberryi, *and* A. lucasanus

Species	Sex	Series of body-rings	Remarks
A. aequalis, from Matamoros, Mexico (U.S.N.M. No. 11599).	♀	11+17+8=36	Carapace rough with small spines, spines on carina.
	♀	11+19+8=38	Carapace smooth, no spines on carina.
A. aequalis, from Matamoros, Mexico (U.S.N.M. No. 58769).	♂	11+16+11+i=38+i	Carapace smooth, no spines on carina. Two spines on hind margin of telson, as described for *A. longicaudatus*.
A. newberryi, from Utah (U.S.N.M. No. 11601).	♀	11+19+10=40	Carapace with few, very small spines. Five central spines on telson (*a*, fig. 29), some minute spines also.
Do	♀	11+19+10=40	Carapace rough, many small spines on carina. Four central spines on telson (*b*, fig. 29), minute spines also.
A. lucasanus, from Cape San Lucas, Baja California, Mexico (U.S.N.M. No. 11602).	♂	11+19.5+10.5+spiral of a little more than 2 rounds=41+sp.	Carapace smooth, no spines on carina.
A. lucasanus (paratypes), from Kansas (Stockholm Museum).	♀	11+19+9=39	All specimens—carapace smooth, no spines on carina.
	♂	11+16+11=38	
	♂	11+16+11+i=38+i	
	♂	11+16.5+11.5=39	
	♂	11+17.5+10.5=39	
	♂	11+18+11=40	
	♂	11+16+2+sp. 2r.+6+sp. 2r.=35+sp. (pl. 7, figs. 1, 2).	

were sent to the Stockholm Museum show the patterns of three of his species. I have not found any correlation between any one pattern and other characters.

One feature considered here, in a limited way only, is the presence of spines at the dorsal hind margin of the telson. Two spines should be characteristic of *A. longicaudatus*. Even in this respect there is often a great variation (fig. 30). Sometimes there are a number of small spines on this margin, sometimes only a few or none at all, and in some specimens we find two relatively large spines placed near the midline. We notice that such spines occur not only in the pattern said by Packard to be characteristic of *A. longicaudatus*, but also in one which, as far as the central spines are concerned, is given for *A. lucasanus*. Here, too, I have looked in vain for correlation with other characters.

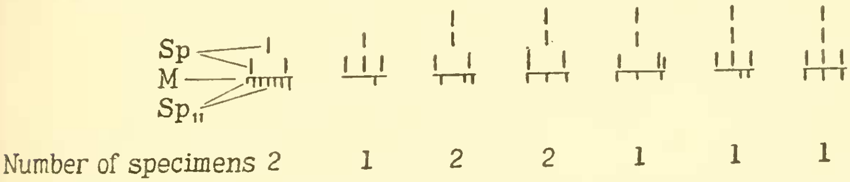


FIGURE 30.—Patterns of dorsal central spines and spines on dorsal hind margin of the telson in specimens of *Apus longicaudatus* LeConte, from California (*A. oryzaphagus* Rosenberg and *A. biggsi* Rosenberg). Abbreviations as in figure 29.

Extra-American species of the genus, too, present great variation in the spines on the telson. Often it is even greater than in American species, as I have found in *A. australiensis* and *A. granarius*. Barnard (1929) arrived at the conclusion that the presence, absence, or varying degree of development of the central spines is of no taxonomic significance in South African forms.

Summing up, I have found that the main characters used by Packard when describing his species of *Apus* are in part wholly unreliable and in part subject to considerable variation without any clear correspondence to other characters. Further, intermediate forms occur very often.

I have examined Packard's type specimens in the U. S. National Museum and also paratypes of *A. lucasanus* in the Stockholm Museum. Some of their characters are given in table 7. The variations in the number of legless rings and the armature of spines on the telson of *A. lucasanus* are already accounted for, and we learn from this that Packard did not pay any attention to the presence or absence of spines on the carapace and its carina. I quite agree with him that this character is of no taxonomic significance. Further, we notice from table 7 that the male of *A. aequalis* has two spines at the hind margin of the telson, a character given by him for *A. longicaudatus*.

TABLE 8.—*Total number of body-rings observed in specimens of* Apus longicaudatus *LeConte from various localities* [1]

Locality [1]	U.S.N.M. No.	Number of specimens	Males													Number of specimens	Females																		
			38	+i	39	+i	40	+i	41	+i	42	+i	43	+i	44		34	+i	35	+i	36	+i	37	+i	38	+i	39	+i	40	+i	41	+i	42	+i	43
California (Paratypes of *A. oryzaphagus*)	88360															6		x	x																
California (Paratypes of *A. biggsi*)	88361															4				x	x														
Galápagos Islands	84240															2				x			x												
Mexico (Types of *A. aequalis*)	11599															2					x				x										
New Mexico	41842															2								x				x							
General Acha, Argentina (Stockholm Mus.)																6										x	x								
Kansas (Paratypes of *A. lucasanus*, Stockholm Mus.)		6	x	x	x		x									1											x								
Nevada	85524	1	x																																
Mexico (Type of *A. aequalis*)	58769	1		x																															
Colorado	30576															2											x		x						
Texas	61750	20						x	x	x	x	x	x			12											x		x	x	x		x		
Oregon	41845															2												x	x						
Wyoming (?)	58766	33							x	x	x	x	x	x	x	98												x	x	x	x	x	x	x	x
Utah (Types of *A. newberryi*)	11601															2													x						
Texas	79027															1													x						
Montana	63289	1									x																								
Mexico (Type of *A. lucasanus* with spiral)	11602	1											x																						

[1] For details, see tables 6 and 7 (pp. 58, 60).

As I have said, the presence of such spines will not do as a specific character.

The total numbers of body-rings in table 7 might give the impression that we have, at last, found a distinguishing character for *A. aequalis* in its relatively low number. This would tally well with Packard's statement that this species has a short body in relation to the length of the carapace and that comparatively few rings are

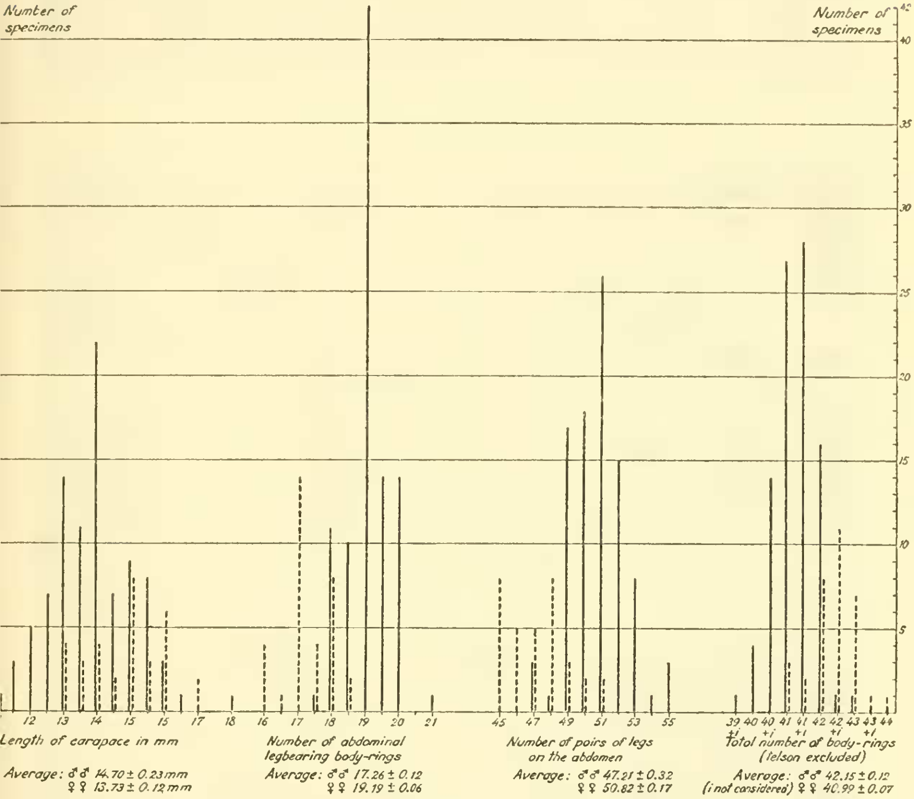


FIGURE 31.—Variations in the length of the carapace, number of legs, number of abdominal leg-bearing rings, and total number of rings in a population of 33 males and 98 females of *Apus longicaudatus* LeConte, from near Aurora, Wyo. (U.S.N.M. No. 58766). Males indicated by dashed lines, females by solid lines. Correlations of various kinds to be considered in a later paper.

exposed beyond the carapace. But a look at the paratypes of *A. lucasanus* contradicts this conclusion. There is a male with the same number as the type specimen of *aequalis* (38+i), and others with a little lower or higher number. The female has a number which is only slightly higher than that of the types of *A. aequalis*. As I have found (see table 8), the total number of rings in American forms of *Apus* present a continuous series from 34+i to 43 in the females and from 38 to 44 in the males. We cannot divide the series into species at some points arbitrarily chosen. And we know that the variation in this respect may be quite considerable.

It seems clear that Packard's species *A. aequalis*, *lucasanus*, and *newberryi* cannot be upheld. All these forms ought to be included in *A. longicaudatus*, which was described first.

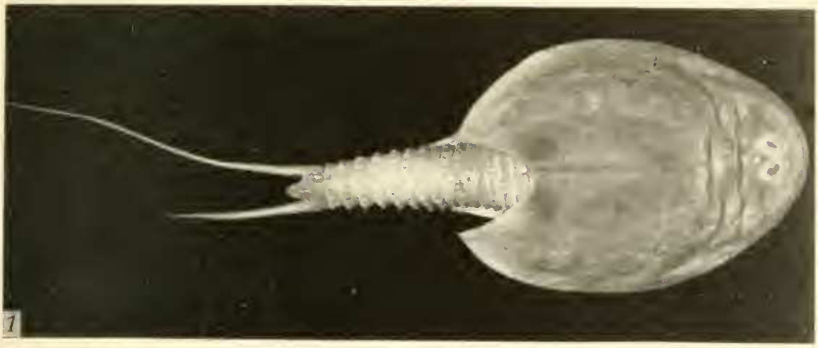
In this species I also include Rosenberg's species *A. oryzaphagus* and *biggsi*. These two forms differ from each other in two points, according to the description. The former species should have 35 body-rings (34+i or 35 in paratypes examined by me) and be small; the latter should have 36 rings (35+i or 36 in paratypes examined by me) and be larger. Considering the continuous series of variation of the number of rings in American forms it seems difficult to accept a certain number as a specific character. Similar numbers are observed, even in other samples, as table 8 demonstrates. One of the types of *A. aequalis* has exactly the same number as *A. biggsi* (table 8). The taxonomical value of the differences in size is doubtful. The forms in question are probably nothing more than populations with a pronounced parthenogenetic tendency, counterparts of which are to be found in the European species, *A. cancriformis*. In all respects, they join the series of variation in other American forms. Parthenogenetic populations probably also occur in the Galápagos Islands, from which locality I have seen lots (U. S. N. M. Nos. 83031, 82033–5, and 84240) totaling several hundred specimens, all female. Table 8 lists other localities from which only females have been found, but the material is too scanty to permit any conclusions about the possible existence of parthogenesis.

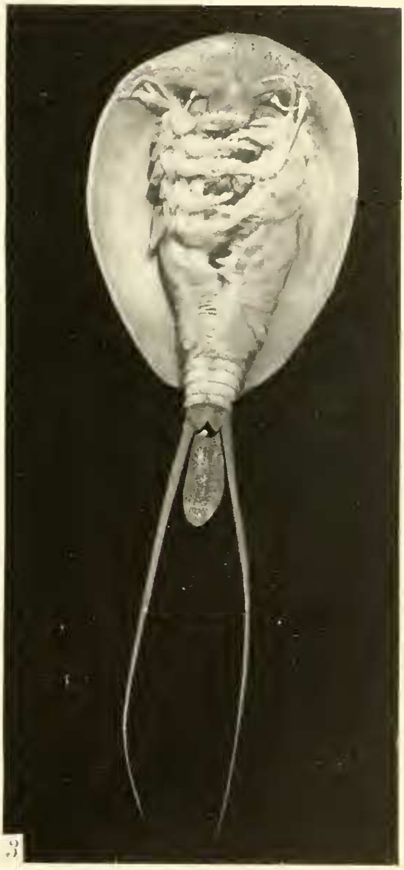
I have not had access to specimens of *A. domingensis* Baird from Haiti or *A. guildingi* Thompson from St. Vincent Island (Packard, 1883, p. 326), and so I cannot say anything of the taxonomic status of these forms except that no facts in the short descriptions contradict an assumption that they belong to *A. longicaudatus*.

Apus longicaudatus, in this sense, is very variable. So are other species of the genus, too, according to my experience. In one respect the variation seems to be remarkably great here, and that is the total number of rings in the females (34+i to 43). It is true that I have not observed such a great range of variation in other species (see table 4), but we must not forget that only relatively limited material of the other species is considered here. How great a variation they really have remains an open question.

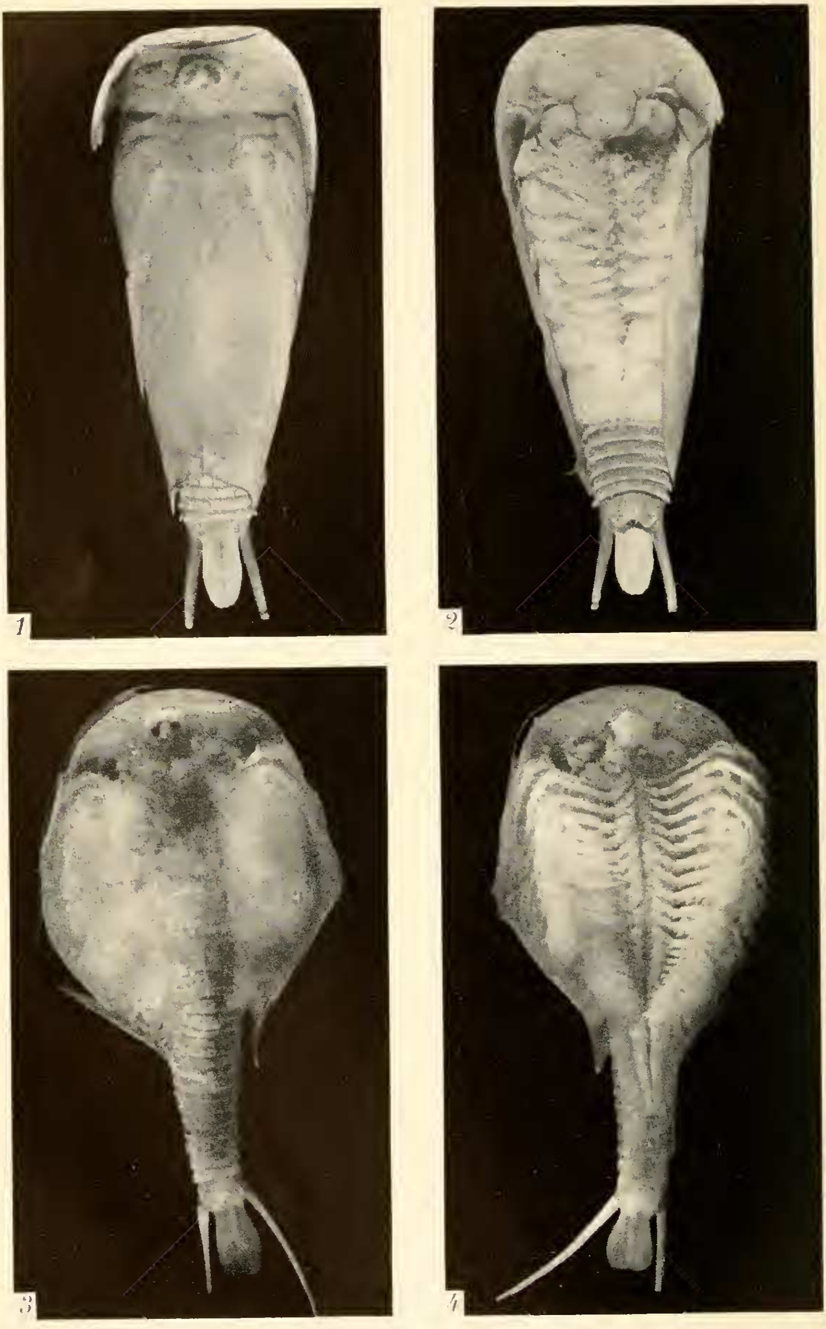
The future may show into what units *A. longicaudatus* can be divided. Not even their taxonomic value can be predicted, though, from the standpoint of our present knowledge, it seems unlikely that they will be species.

It seems clear that *A. longicaudatus* is closely related to several

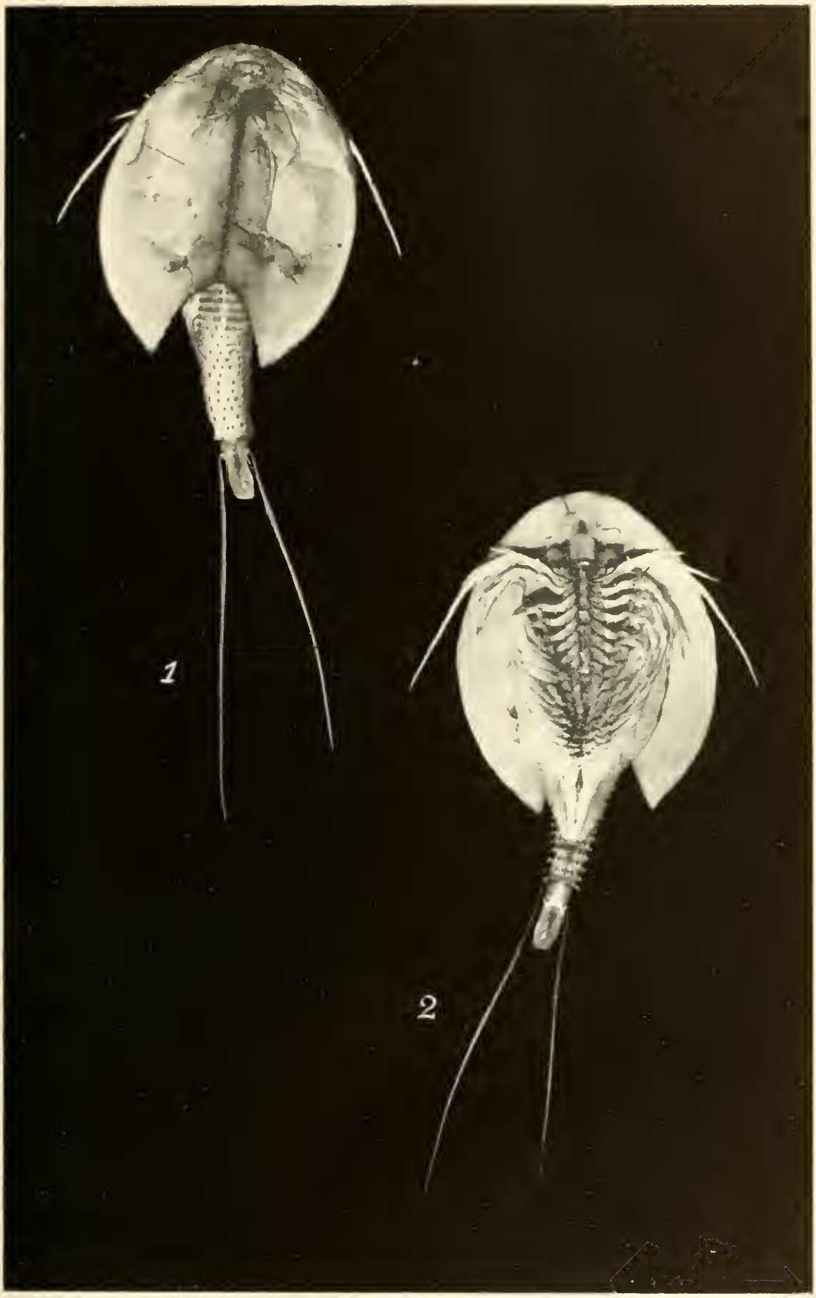




1. *Lepidurus arcticus*, ♀, from Ooglamie, Alaska (U.S.N.M. No. 7903), dorsal view, × 4.
2, 3. *Lepidurus couesii*, ♂, from Montana, cotype (Stockholm Mus.), dorsal and ventral views, × 3, endites of first pair of legs partly broken.

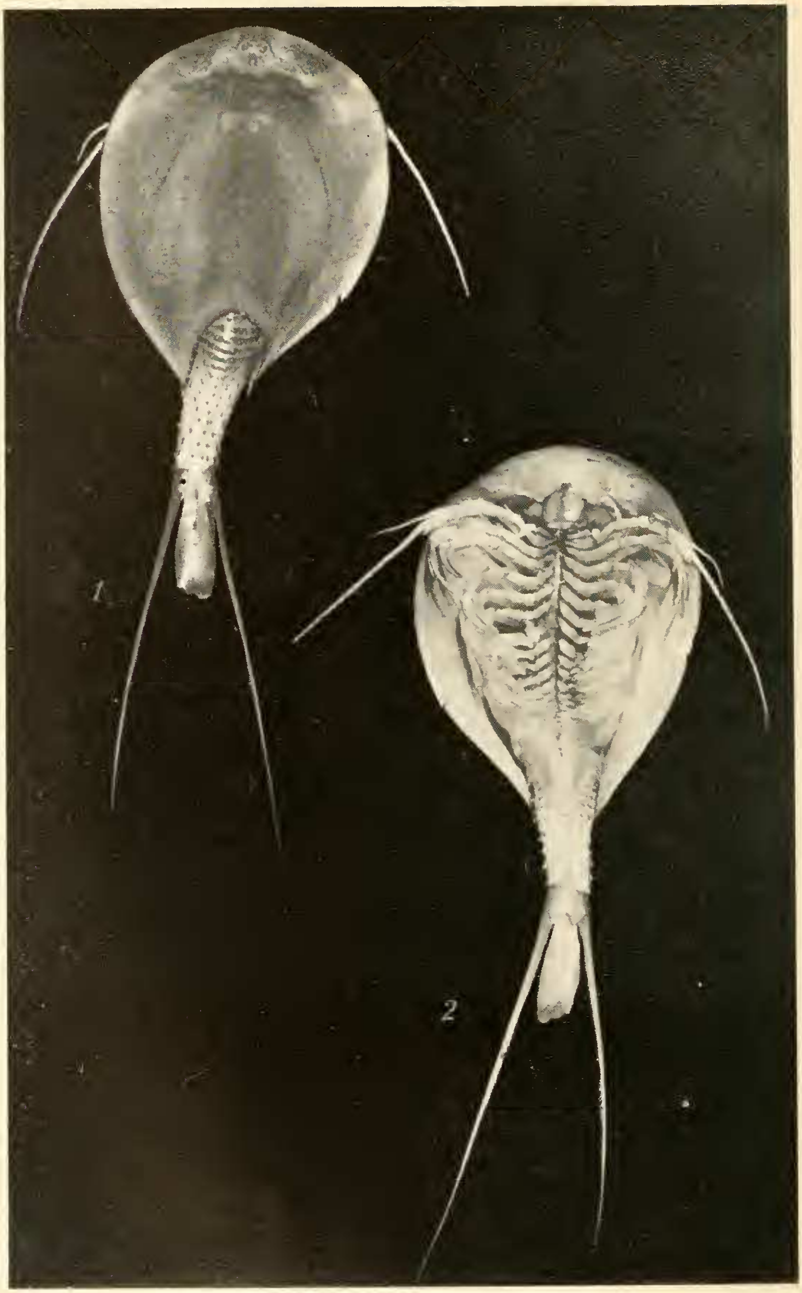


1, 2. *Lepidurus packardi*, ♀, from California, holotype (Paris Mus.), dorsal and ventral views, × 4.
3, 4. *Lepidurus bilobatus*, ♀, labeled "Type, Utah, coll. Henshaw" (U.S.N.M. No. 11606), dorsal and ventral views, × 3.



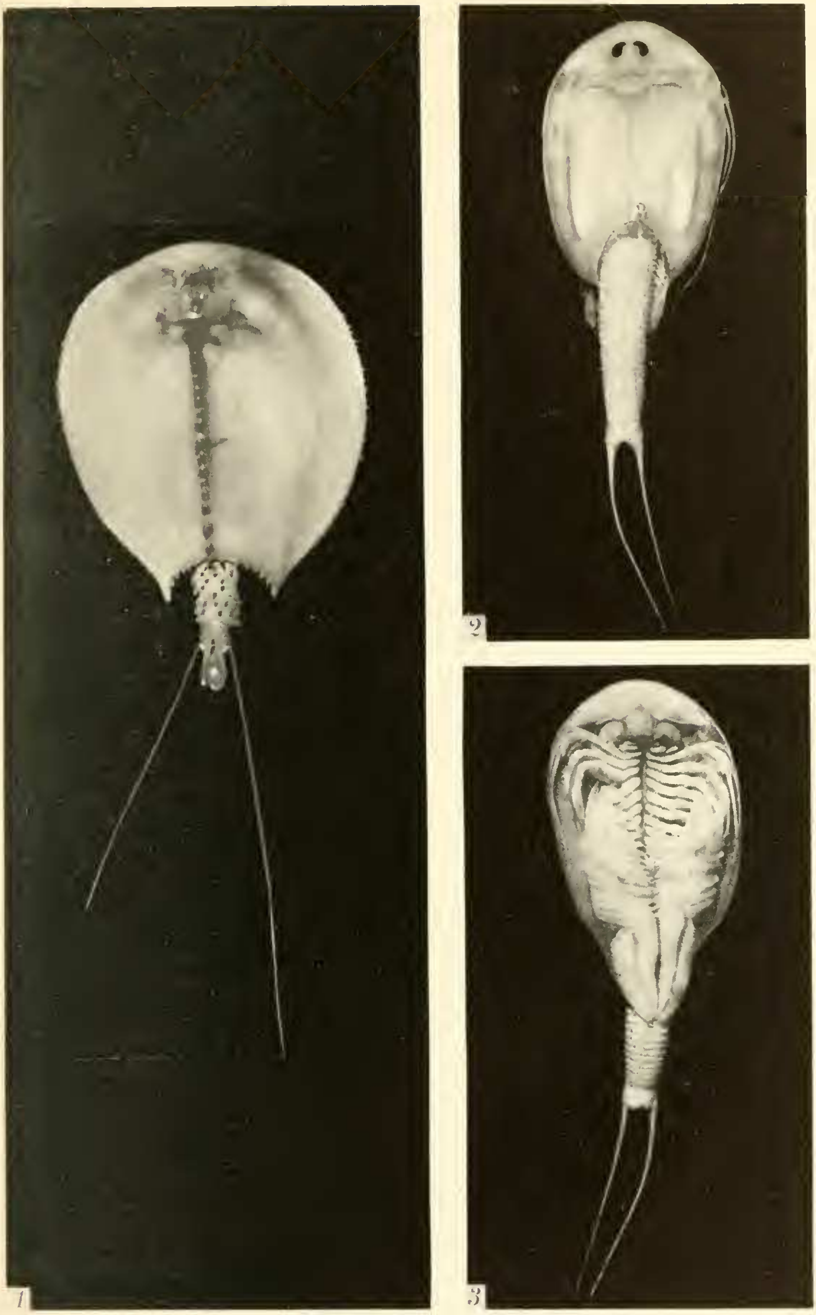
Lepidurus lynchi, new species.

Female, from Upper Grand Coulee, Wash., holotype (Uppsala Mus.), dorsal and ventral views, × 2.



LEPIDURUS LYNCHI, NEW SPECIES.

Male, from Upper Grand Coulee, Wash., allotype (Uppsala Mus.), dorsal and ventral views, × 2.3.



1. *Lepidurus lynchi echinatus*, new variety, ♀, from Goose Lake, Lakeview, Oreg., paratype (Uppsala Mus.), dorsal view, × 2.
2, 3. *Apus longicaudatus*, ♀, from General Acha, Argentine (Stockholm Mus.), dorsal and ventral views, × 2.